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Co-variations between plant functional traits emerge from constraining parameterization of a terrestrial biosphere model.

Running title: Functional traits variability inferred from data assimilation


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Key words: Plant functional traits, ORCHIDEE, terrestrial model, optimization, data assimilation, plant acclimation.

Abstract

Aim

Mechanisms of plant trait adaptation and acclimation are still poorly understood and consequently lack a consistent representation in terrestrial biosphere models (TBMs). Despite the increasing availability of geo-referenced trait observations, current databases are still insufficient to cover all vegetation types and environmental conditions. In parallel, the growing number of continuous eddy-covariance observations of energy and CO₂ fluxes has enabled modelers to optimize TBMs with these data. Past attempts to optimize TBMs parameters mostly focused on model performance overlooking the ecological properties of ecosystems. The aim of this study is to assess the ecological consistency of optimized trait-related parameters while improving the model performances for gross primary productivity (GPP) at sites.

Location

World

Time period

1992-2012

Major taxa studied

Trees and C3 grasses
Methods

We optimized parameters of the ORCHIDEE model against 371 site-years of GPP estimates from the FLUXNET network and we looked at global co-variation among parameters and with climate.

Results

The optimized parameter values are shown to be consistent with leaf-scale traits, in particular well-known trade-offs observed at the leaf level, echoing the leaf economic spectrum theory. Results show a marked sensitivity of trait-related parameters to local bio-climatic variables and reproduce observed relationships between traits and climate.

Main conclusions

Our approach validates some biological processes implemented in the model and enables us to study ecological properties of vegetation at the canopy level, as well as some traits that are difficult to observe experimentally. This study stresses the need for 1) implementing explicit trade-offs and acclimation processes in TBMs, 2) improving the representation of processes to avoid model-specific parameterization as well as 3) performing systematic traits measurements at FLUXNET sites in order to gather information on plant ecophysiology and plant diversity, together with micro-meteorological conditions.
Introduction

Terrestrial biosphere models (TBMs) describe the different processes controlling exchanges of energy and trace gases between the atmosphere and the biosphere. Process-based TBMs are useful tools for understanding the dynamics of ecosystems under changing environment, for present-day to future conditions.

In most TBMs, the worldwide vegetation is divided into plant functional types (PFTs) based on general characteristics of the photosynthetic pathways, phenology, structure and physiology. Different PFTs usually share the same equations but use different parameter values to describe generic processes (photosynthesis, respiration), while biome-specific equations may be used for phenology and allocation. Therefore, for a given PFT, only the differences in climate and soil properties can determine spatial and temporal gradients in ecosystem state variables.

The prescribed values of PFT-specific parameters are derived from discrete observations obtained at varying spatial scales (organs, individuals, ecosystems; Reich et al., 2007; Kattge et al., 2009) and in specific environmental conditions, despite the modulation of real world plant traits by climate (Wright et al., 2005; Ordoñez et al., 2009; van Ommen Kloekke et al., 2012; Maire et al., 2015) and soil properties (Fisher et al., 2012). In addition, some TBM parameters relate to traits that are difficult to measure experimentally (e.g. root turnovers or carbon allocation), or are model-specific. These parameters can hardly be directly optimized from observations and their adjustment to varying environmental conditions can only be determined by labor intensive multi-factorial ecosystem manipulation experiments (Luo et al., 2017). This rigid determination of parameter values, combined with the use of single PFT to cover a range of different species (Peaucelle et al., 2016), hinders a realistic representation of the past, present and future ecosystem dynamics both at the local or regional scale, and their
response to global drivers such as climate, elevated CO$_2$ and nutrient fertilization (Hartig et al., 2012, Atkin et al., 2015; Kroner & Way, 2016; Reich et al., 2016).

To overcome the rigidity of the PFT representation, various approaches have been proposed to provide continuous distributions of plant functional traits related to model parameters. These approaches range from extrapolating trait observations across spatial gradients (Verheijen et al., 2015), to estimating optimal trait values according to ecological theories and plant-centered approaches (Reu et al., 2011; Pavlick et al., 2013; Prentice et al., 2014). The drawback of these different approaches is that they require both spatial and temporal observations for model calibration and/or validation. Despite the increasing number of georeferenced trait observations (Kattge et al., 2011), current databases are insufficient to cover all vegetation types and environmental conditions for projections at the ecosystem level (Musavi et al., 2015, 2016). Moreover, trait observations should be co-located with process and meteorology data to understand linkages between traits and ecosystem function (Law et al., 2008), which is rare in existing databases although increasingly addressed for some biomes (Bjorkman et al., 2018). Long-term monitoring of functional traits is needed to assess the adjustments to climate. As such information is still lacking, approaches have been developed that confound the spatial and temporal dimensions of trait variability.

Another modeling strategy consists in optimizing TBMs against observed variables sensitive to ecosystem-level parameters in order to overcome these limitations. This approach assumes that the model structure is unbiased, so that realistic parameters values can be estimated when model simulations best match observations. Because biometric variables are sparse and often depend on processes not represented in models (Thum et al., 2017), energy and trace gas flux measurements are more appealing to optimize TBM parameters. Eddy-covariance data provide near-continuous observations of CO$_2$, latent heat and sensible heat fluxes, and are therefore well suited for better constraining photosynthesis, respiration, transpiration and...
carbon phenology model parameters. Eddy-covariance measurements have been extensively used to improve specific performances of TBMs, i.e. their ability to reproduce specific observed ecosystem behaviors (Carvalhais et al., 2010; Kuppel et al., 2012; Santaren et al., 2014; Schürmann et al., 2016). However, such model calibrations are disconnected, by construction, from ecological theory or trait-based relationships, and do not exploit the full potential of continuous flux observations across the globe, which provide both spatial and temporal information.

In this study, we aim at assessing the consistency of model trait parameters optimized against eddy-covariance flux tower measurements of growth primary productivity (GPP) using the state-of-the-art ORCHIDEE land surface model (Krinner et al., 2005). In addition to classical optimization analyses (i.e. looking for the optimal parameter sets resulting in the highest model improvement), we focus here on the variability of optimized parameter values and on inter-trait correlations or trait-environment correlations. By doing so, we address the following research questions: 1) Are the parameters retrieved by optimizing the model against flux tower records consistent with known relationships between traits (i.e. trade-offs)? or 2) between traits and environmental variables? and 3) What new relationship can be identified with this approach?
Methods

The ORCHIDEE model

The land surface model ORCHIDEE (v1.9.6, without nitrogen cycle) computes biosphere-atmosphere exchanges, consistently with water and carbon storage using ordinary differential equations (Krinner et al., 2005) (Figure1). Given meteorological forcing, plant and soil conditions, the model simulates photosynthesis, all components of the surface energy budget and hydrological processes at a half-hourly time step, while the dynamics of carbon storage are calculated daily. In ORCHIDEE, the land surface is discretized into 12 plant functional types (PFT) and bare soil (Table S1.1, Appendix S1). All PFTs share the same equations, but use different parameter values, except for phenology (budburst/senescence), which is PFT-specific (Botta et al., 2000).

Eddy-covariance GPP

We used half-hourly flux observations from eddy-covariance sites within the FLUXNET network (https://fluxnet.fluxdata.org). The sites were selected on the basis of spatial homogeneity and the dominance of a vegetation type that could easily be matched to one of the PFTs in ORCHIDEE, excluding crops and C$_4$ grasses. The vegetation type information at each site was obtained from http://fluxnet.ornl.gov. The list of analyzed FLUXNET sites (98 sites, 371 site-year) and the corresponding PFTs is given in Appendix S2. The following analyses rely on GPP derived from net ecosystem exchange (NEE; reference with variable USTAR threshold) after accounting for ecosystem respiration calculated using the method of Reichstein et al., (2005) provided in the FLUXNET dataset. Years with less than 80% of available half hourly observations were discarded.
**Meteorological data**

Because ORCHIDEE needs continuous half-hourly meteorological forcing, we gap-filled time series of weather variables using the interpolation algorithm developed by Vuichard & Papale (2015). Linear interpolation was applied between available observations when the gap-duration in the meteorological data was less than six hours. Otherwise, the variables were interpolated and bias corrected using the ERA-interim reanalysis (~80km, Dee et al., 2011).

Snow and rain were identified according to air temperature (threshold for snow being 0°C).

**Data assimilation procedure**

The parameters of ORCHIDEE were optimized with the ORCHIDAS package developed by: Kuppel et al., (2012); Bacour et al., (2015); MacBean et al., (2015) and Peylin et al., (2016); (https://orchidas.lsce.ipsl.fr/; Figure 1). Gaussian distributions of parameter and observation errors being assumed, a gradient-based approach was used to minimize the Bayesian cost function $J$ (Tarantola, 2005):

$$J(x) = \frac{1}{2} \left[ (y - H(x))^\top R^{-1} (y - H(x)) + (x - x_b)^\top B^{-1} (x - x_b) \right]$$

This function quantifies the difference between observations ($y$) and simulations ($H(x)$) (here GPP), and between *a priori* ($x_b$) and optimized parameters ($x$). The $B$ and $R$ matrices are the prior error covariance matrices for parameters and observations, respectively (including in the latter case eddy-covariance measurement and model errors).

Both $R$ and $B$ were taken as diagonal, as discussed in Kuppel et al. (2012). The $J(x)$ function was iteratively minimized with the L-BFGS-B algorithm (Byrd et al., 1995), which notably allows bounding the range of variation of the parameters to optimize. After model calibration (i.e. minimizing $J$), the posterior error covariance matrix ($A$), providing the full statistical distribution of the optimized parameters was estimated by:
where $H$ is the Jacobian of model at the minimum of $J$ (Tarantola, 2005). The covariances of
errors between parameters contained in the non-diagonal terms of $A$ inform about the ability
of observations given the structure of $H$ to solve for parameters individually, or in
combination. High error covariance between two parameters relates to the equifinality
problem, whereby different values of these parameters result in model outputs equally
matching the observations (relative to $R$).

**Optimized parameters**

We restricted our exercise to the parameters involved in the assimilation of CO$_2$ following
previous sensitivity analyses from Kuppel (2012). We analyzed 14 parameters controlling
long-term and inter-annual GPP variability (Table 1). The key equations involving each
optimized parameter as well as their effect on the simulated GPP are described in Table S1.2
(Appendix S1). The parameters were related to photosynthetic capacity, phenology, carbon
allocation and the water budget. Photosynthetic capacity parameters were the maximal rate of
carboxylation limited by CO$_2$ ($V_{cmax}$), the ratio between the maximal rate of carboxylation
limited by light and $V_{cmax}$ ($V_j/V_c$), the optimal temperature of photosynthesis ($T_{opt}$) and the
slope of the Ball-Berry model for stomatal conductance ($g_{slope}$). Parameters driving
phenology were the specific leaf area ($SLA$), leaf longevity ($Lage$), summer maximal leaf area
index ($LAI_{max}$) and the temperature for leaf senescence ($C_{senes}$). Allocation parameters were
the minimal fraction of $LAI_{max}$ for the use of carbohydrate reserves ($K_{lai}$) and the period
after budburst during which the use of carbohydrates is allowed ($tau_{leaf}$) for the formation of
new leaves. Finally, two parameters involved in the water status of the plant were the
exponential factor describing the root profile and length ($K_{root}$) and the minimal threshold at
which photosynthesis becomes limited by minimum water potential ($W_{lim}$). In addition, two
scaling factor $K_{bm}$ (initial biomass of leaves for evergreen species) and $bbdate$ (spring burdburst date) were added in the optimization to allow adjusting the seasonal timing of GPP.

The range in variation of the three parameters corresponding to observable traits ($SLA$, $V_{cmax}$ and $Lage$) was set from the TRY database for each PFT (Niinemets et al., 1999; Deng et al., 2004; Meir et al., 2007; Kattge et al., 2009, 2011; Domingues et al., 2010; Cernusak et al., 2011; Azevedo & Marenco, 2012; van de Weg et al., 2012; Nascimento & Marenco, 2013). Species from the TRY database were assigned to corresponding PFTs based on available metadata about plant structure, leaf phenology and climate information extracted from species' latitude and longitude coordinates. We chose as a reference range the 2.5 - 97.5 percentile of the trait distributions from TRY. The variation ranges for the other parameters were fixed based on expert judgment (Kuppel et al., 2014).

**Simulations and assimilation set-up**

At each flux tower site, we assumed that the eddy-covariance flux footprint was entirely composed by a single PFT (Appendix S2). The model was forced by local meteorological observations (see Meteorological data section) and soil texture from the harmonized worldwide soil database (Nachtergaele et al., 2012) to define the residual and saturation water contents, and the saturated hydraulic conductivity in the soil model (Ducoudré et al., 1993; Krinner et al., 2005) based on Van Genuchten (1980). Initial soil carbon pools in equilibrium with local climate were obtained with an analytical spin-up procedure (Lardy et al., 2011; Xia et al., 2012). Initial biomass was simulated until reaching equilibrium (generally after a ~300 year-long simulations using the studied year meteorological data and constant $CO_2$ set to level of the year), thus different from the real stand age observed at each site.
We optimized GPP averaged over 15 days using moving windows to avoid noise from high frequency variations in the parameter optimization that could induce convergence issues (Bacour et al., 2015). As far as test data from eddy-covariance measurements are concerned, high frequency variations in fluxes include also variation in the boundary layer that are unrelated to the fluxes at the surface (Ibrom et al., 2006). Santaren et al. (2007) estimated that for parameters related to photosynthesis and phenology, optimization based on half-hourly observations did not improve the results. For each site, the optimizations were conducted year-by-year to account for trait variability over time (Wu et al., 2013).

Following MacBean et al. (2015), each calibration (site-year) used ten replicates representing different starting parameter sets with values randomly picked within their allowed variation range (Table S1.3). Only the best calibration out of these ten replicates was retained for analyses. This procedure increases the chances of finding the global minimum of $J$ as Santaren et al. (2014) showed that the gradient-based algorithm was sensitive to initial conditions with a non-linear and complex model such as ORCHIDEE.

**Analyses**

We only retained calibrations for which the optimized model reproduced GPP observations with high precision. The rationale for this was that optimized parameters from model runs which agreed poorly with GPP observations provided little or no useable information. The filtering was performed using a two-step procedure.

First, the criterion for ‘improved GPP simulation’ was the relative site-year posterior RMSE (RMSE$_{re}$) between observed and optimized GPP:

$$RMSE_{re} = \frac{RMSE}{mean(GPP_{obs})}$$

(4)
Whenever the value of RMSE_{re} was higher than the all-RMSE_{re} median plus one interquartile range (IQR), the site-year was removed from the analysis. We also discarded sites with ‘inconsistent parameters values’, i.e. with too large differences between the ten replicates at the same site reflecting convergence issues (equifinality) of the algorithm.

Secondly, for sites with at least two RMSE_{re} below 10 % among the ten replicates, we estimated the coefficient of variation (CV) of parameters across the replicates. We retained only years for which the median CV was below the median of all CV plus one IQR of their distribution. This filtering provided optimized parameters from 371 site-years (over 516 initially considered) for 98 sites (over 116; Appendix S2) spanning seven PFTs located in boreal, temperate and tropical areas (Table S3.4; Appendix S3).

For each parameter, we calculated the uncertainty reduction (UR) as:

\[ UR = 1 - \frac{\sigma_{post}}{\sigma_{prior}} \]  

With \( \sigma_{post} \) and \( \sigma_{prior} \) being the posterior and prior parameter uncertainties (square root of the diagonal elements of \( A \) and \( B \)). We then separated in the analysis the well- from the poorly-constrained parameters. Well-constrained parameters are defined as those with 1) \( UR \) higher than the median of \( UR \) distributions for all parameters and 2) a low correlation of error with other parameters (from the A matrix, Eq. 2). Note that a strong error correlation making two parameters poorly constrained individually is still an interesting result as it indicates a range of possible tradeoffs between these two parameters.

The optimized parameter values were regressed against the local background bio-climatic variables (Table 2) for each site, and against the soil relative water content (volume of water by volume of soil) simulated by ORCHIDEE. Bio-climatic variables were averaged over the whole year and over the length of the growing season (GSL). For temperate sites, the growing
season was defined as the period with daily temperature above 5°C and relative soil water content above 0.2 (Violle et al., 2015). In some tropical regions, the growing season length is potentially limited by water availability (wet/dry seasons), we thus kept the same definition as for temperate ecosystems. For boreal sites, we adapted the definition of the growing season such as weekly temperature must be above 0°C. Analyses were performed with the R.3.2 software (R Core Team, 2016) and standardized major axis (SMA) analyses were performed with the 'lmodel2' package (Legendre, 2014). Because we sought to compare simulated correlations with common ecological properties observed at the global scale, we analyzed different groups of PFTs: all PFTs together; deciduous versus evergreens; needleleaves versus broadleaves; and C₃ grasses (Table S1.1). Regressions were performed both with and without a logarithmic transformation of the data.
Results and comparison to existing literature

Optimization performances

A full description of the optimization performances and parameter uncertainty reduction can be found in Appendix S3.

In all cases, the optimized GPP time series better agrees with observations than the prior ones, with the RMSE being reduced by 76.6 ± 13.0 % (Table S3.4; Appendix S3). The median posterior RMSE is 0.19 and the IQR is 0.11. The median CV over all parameters is 0.24 (IQR=0.13). After optimization, the parameter uncertainty (Eq. 5) is reduced by 30 % on average (Table S3.5; Appendix S3).

The posterior error correlation matrix A (Eq.2) reveals a positive correlation between $V_{cmax}$ and several other parameters including (Figure 2): $Topt$ ($r=0.57\pm0.05$); $gslope$ ($r=-0.37\pm0.04$); $Kroot$ ($r=0.24\pm0.07$) and $Vj/Vc$ ($r=-0.31\pm0.04$). There also exists a negative correlation between $Kroot$ and $gslope$ ($r=-0.38\pm0.08$), between $Kroot$ and $Wlim$ ($r=-0.30\pm0.09$) and between $LAImax$ and $Klai$ ($r=-0.37\pm0.16$) (Figure 2).

Jointly analyzing information from the uncertainty reduction (Appendix S3) and the cross-parameter error correlation enables to distinguish between: 1) well constrained parameters ($Lage$ and $SLA$ for evergreens/ $Lage$ and $Csenes$ for deciduous); 2) well constrained parameters with a risk of equifinality ($gslope$, $Kroot$, $LAImax$, $Topt$ and $V_{cmax}$); and 3) poorly constrained parameters ($Vj/Vc$, $Klai$, $Tauleaf$ and $Wlim$; Table 1). In the following analyses, trait co-variations have to be interpreted in respect to confidence intervals (posterior error) in parameter estimates.

Co-variation between parameters

We analyzed cross-site correlations between optimized parameters in relation to expected trait relationships. The co-variation between all parameters is illustrated in Figure S4.2 (Appendix
For more clarity and considering the large number of parameters, we only describe here the relationships involving four parameters related to phenology (SLA, \(L_{age}\)) and photosynthesis (\(V_{cmax}\), \(g_{slope}\)). All relationships are provided in Table S4.6 (Appendix S4).

We observed a negative correlation between SLA and \(L_{age}\) for all PFTs (\(r=-0.63\); Table 3) as well as for evergreens (\(r=-0.67\)) and broadleaves PFTs (\(r=-0.53\)), separately. The slope of the emerging relationship between \(L_{MA}\) (1/SLA) and \(L_{age}\) (1.91; 1.63-2.24 95% confidence interval; \(p < 0.05\)) for all PFTs was close to the observed slope from field observations (1.71; 1.62-1.82; Wright et al. 2004). Results highlighted other co-variations between \(L_{age}\) and \(V_{cmax}\) (\(r=-0.59\) overall PFTs), \(g_{slope}\) and \(L_{age}\) (\(r=-0.7\) for broadleaves), \(LAI_{max}\) and SLA (\(r=0.6\) for needleleaves), and between SLA and \(V_{cmax}\) (\(r=-0.55\) for evergreens). Here again, the slope between \(L_{age}\) and \(V_{cmax}\) emerging for broadleaves PFTs (-1.69) was close to observations (-1.13; Xu et al. 2017).

No relationships were reported between \(g_{slope}\) and \(L_{age}\) or between \(g_{slope}\) and SLA, but a trade-off between the stomatal conductance (\(gs\)) and \(L_{age}\) was observed experimentally (Reich et al., 1992; Poorter & Bongers, 2006), as well as a positive correlation between \(gs\) and SLA (Poorter & Bongers, 2006). The optimizations showed opposite relationships between \(g_{slope}\) and SLA depending on the PFT: a positive significant correlation was obtained for deciduous PFTs and a negative significant correlation for evergreens and grasses (Table 3).

The positive relationship between SLA and \(LAI_{max}\) emerging from optimized parameters for coniferous PFTs was consistent with the positive correlation between \(LAI\) and SLA reported by Pierce et al. (1994) for coniferous forests. Finally, a negative correlation between SLA and \(V_{cmax}\) has been observed experimentally for two gymnosperms species (Niinemets et al., 2007), confirming the negative relationships found in our study for needleleaves. Despite the
equifinality risk between gslope and the soil water stress Wlim in Figure 2, the positive correlation observed for broadleaves (r=0.7) and evergreens (r=0.52) was comparable to observations from independent data compiled by Lin et al. (2015).

Other significant correlations from the optimized parameters (Table S4.6, Figure S4.2; Appendix S4) could not be verified against observations because of the correlation of errors observed in Figure 2 or because of the scarcity of ecological data preventing us to conclude about the true nature of those correlations, as for example between gslope and Vcmax.

Variation of trait-related parameters with climate

We analyzed correlations between parameters and climate variables (Table 4, Figure S5.4; Appendix S5). As for co-variations between parameters, we only described here those implying SLA, Lage, Vcmax and gslope. All relationships are listed in Table S5.7 and more detailed analysis are available in Appendix S5.

We found a strong negative correlation between leaf lifespan (Lage) and temperatures (MAT, TMIN; r=-0.78/-0.65; Figure 3a) for evergreen PFTs. This correlation was independently reported at global scale (Wright et al., 2005; van Ommen Kloke et al., 2012) and confirmed by Reich et al. (2014) who showed higher needle longevity with cold temperatures for boreal species. However, the observed positive correlation between Lage and MAT at the global scale for deciduous PFTs (Wright et al., 2005; van Ommen Kloke et al., 2012) was not found specifically for deciduous systems in our study. Nevertheless, a positive correlation was observed for C₃ grasses and broadleaves (including deciduous). We also found a strong negative correlation between Lage and the mean annual precipitations (MAP) for evergreens PFTs (r = -0.65), consistent with field data (van Ommen Kloke et al., 2012). In addition, a
negative correlation between $L_{age}$ and incident shortwave radiation (SW) for evergreens was obtained, consistent with field observations (Poorter & Bongers, 2006).

Regarding SLA, we found opposite sensitivities to $MAT$ for evergreen ($r=0.65$) and deciduous forests ($r=-0.55$). This result is consistent with independent leaf-scale data showing a positive correlation between SLA and $MAT$ for evergreen species (Figure 3b) and a negative correlation for deciduous ones (Wright et al. 2005). The model calibration also resulted in a positive correlation between the relative precipitation ($RELP$; Table 2) and SLA for deciduous trees ($r = 0.60$; Figure 3c). Regarding the positive correlations obtained between SLA with $K_{root}$ or $gslope$ (Table 3), it suggests that SLA is highly sensitive to water stress for deciduous trees. For evergreens, positive correlation between SLA and precipitation also emerges when considering the length of the growing season ($MAPgs$, $r = 0.57$; Table 4); which is consistent with trait data (Wright et al., 2005). For evergreens, SLA was positively correlated to SW ($r=0.53$), a relationship observed by Givnish et al. (2004) and Poorter & Bongers (2006).

In their meta-analysis of stomatal conductance parameters from observations of several PFTs, Lin et al. (2015) showed that the slope of the stomatal conductance is positively correlated to the mean air temperature over the growing period and to soil moisture stress. Here, our results show the same correlation between $gslope$ and soil moisture during the growing season ($r=0.71$; Figure 3d) and relative precipitation ($r=0.66$) for deciduous or broadleaved PFTs. On the contrary, we find that $gslope$ is negatively correlated with mean annual precipitation for $C_3$ grasses ($r=-0.59$), and with shortwave radiation for broadleaved PFTs ($r=-0.63$). Medlyn et al. (2011) suggested that $gslope$ is proportional to the photosynthesis compensation point for CO$_2$, and consequently to growth temperatures of the plant (Bernacchi et al., 2001). This
assumption is supported by the data from Lin et al. (2015). In our study, the relationship between $gslope$ and temperature was not supported.

Finally, $Vcmax$ is mostly sensitive to temperature and light for broadleaved PFTs, with a negative correlation observed with $MAT$ ($r=-0.52$) and $SW$ ($r=-0.54$). This result contradicts previous observations by Ali et al. (2015), who suggested a positive correlation between $Vcmax$ and seasonal temperature and light variations.

**Discussion**

**Uncertainties and shortcomings of the approach**

This section provides an overview of possible shortcomings of our approach that may explain some residual mismatch between model and observations. Several factors can impact the optimized value of the parameters, potentially aliasing the observed relationships: 1) flux measurements errors and errors in ecosystem respiration estimates used to derive gap-filled GPP; 2) optimization protocol/setup errors; and 3) model systematic errors deriving from absent or poorly represented processes in the model.

First, we restricted our analysis to GPP. This flux is not directly measured but estimated from NEE measured using the eddy-covariance method with an estimate of ecosystem respiration determined using empirical models (Reichstein et al., 2005), and thus can be biased by several factors (see Appendix S3 for a list of these factors). We chose GPP over a combination of NEE and latent heat or evapotranspiration fluxes, which has often been used to optimize ORCHIDEE (Kuppel et al., 2012; Bacour et al., 2015; Peylin et al., 2016), because it implies the optimization of more parameters related to soil, respiration and energy budget, and therefore increases the risk of equifinality. To reduce the uncertainties, it is
necessary to lower the correlation of errors between parameters by assimilating complementary biophysical variables. For example, assimilating both GPP and LAI estimates at the site level could improve the evaluation of parameters such as SLA or Lager, and consequently improve the estimation of photosynthesis parameters.

Second, the Bayesian framework is based on the assumption that the model/observation errors are random and that the model structure is “true”. Any bias of model structure is expected to be aliased onto the estimated parameters (MacBean et al., 2016) and might therefore impact the retrieved correlations. For instance, missing processes would be compensated during the optimization by adjusting parameters (e.g. light attenuation, vertical distribution of LAI, diffuse light, horizontal light distribution in the stand) to non optimal values. Also, while traits are usually measured at the leaf level, our approach rather focuses on traits at the canopy level (given the structure of ORCHIDEE and the assumed exponential attenuation of light and LAI from top to bottom of canopy (Krinner et al. 2005; Table S1.2), and the assimilation of GPP data). As an additional test, we conducted the above analyses using multi-year instead of single-year observations in order to add more constraints on parameters (see Figure S4.3 & S5.5). The same relationships were found as with single-year observations, thus strengthening our conclusions, showing that spatial correlations are observed even when taking into account a possible temporal variability of traits.

Finally, a wrong representation of species and the lack of representation of representation of traits variability within a community in ORCHIDEE can affect simulated processes, which will ultimately impact the estimated parameter values (see Appendix S3 for a discussion on initial site conditions). Especially, the C₃ grass PFT represents diverse grasslands, with different species, ecophysiology (Adams et al., 2016) and management practices (Merbold et al., 2014). This results in an increased variability and a high range of estimated plant functional traits (Figure S3.1). A refinement of the PFT definition may improve the
robustness of optimizations (for instance by separating natural or semi-managed biomes), or
by distinguishing genera or major species (Peaucelle et al., 2016).

In order to decrease the impact of uncertainty in PFT composition and reduce the correlation
errors between parameters, the use of concomitant observations of traits and carbon fluxes at
the FLUXNET sites would enable a) to constrain known parameters and b) to validate
optimized traits. However, functional trait observations at FLUXNET sites as well as a
precise description of species composition are not yet systematic (Musavi et al., 2015, 2016).

### Ecological consistency of trait relationships

The optimization of model parameters managed to reproduce many known ecological
properties. The optimized parameters consistently matched the well-known relationships
resulting from the leaf economic spectrum theory (LES, Reich et al., 1999; Wright et al.,
2004). Particularly our results align with the trait theory that long lived canopies are
metabolically less active and are consistent with the LES empirical evidence that plants invest
either in structure or photosynthesis (Liu et al., 2010; Reich, 2014).

Our results also reproduced several observed trait-climate relationships at the PFT level.
Globally, evergreen PFT parameters showed a strong dependency on mean annual
temperature and radiation, while parameters for deciduous PFTs exhibited a strong sensitivity
to precipitation and soil moisture over the growing season (Figure S5.4). As postulated by
Reich (2014), climate exerts a control on the average leaf characteristics at the community
level. The observed relationships obtained at the PFT level might reflect, not only differences
in plant response to climate, but also differences in plant community composition (Shi et al.,
2015). These results suggest that both the development of acclimation processes and trait-
based approaches are needed in TBMs if we seek to capture the effect of biogeography on ecosystem characteristics (Lu et al., 2017; Fisher et al., 2018).

Finally, while the results clearly highlight that photosynthesis and phenological mechanisms implemented in ORCHIDEE are robust enough to reproduce known behaviors of several vegetation species, belowground processes still appear poorly represented, which resulted in weakly constrained parameters and trait co-variations inconsistent with literature. These discrepancies are primarily due to a lack in eco-physiological knowledge reflecting the actual difficulty to study belowground ecological processes. The rooting system uses model-specific parameters (Kroot) that are hardly comparable to measured functional traits.

Concluding remarks and recommendations

The approach presented in this study is a new and effective way to validate the processes implemented in TBMs, to better define vegetation response to climate (Liang et al., others, 2018), and could help improving existing data assimilation frameworks (Kaminski et al., 2013; LeBauer et al., 2013; Arsenault et al., 2018) by bringing ecological constraints. The availability of continuous observations from eddy-covariance flux measurements gives a unique opportunity to resolve the different components of the short and long-term variability of traits through this approach.

Our results show that optimized leaf-related parameters align with plant trait theory, and highlight the need to implement acclimation processes and trait-based approaches in models instead of using constant parameters to reduce uncertainties in spatio-temporal patterns of the modeled carbon fluxes. A first step would be to assess the behavior of the model at the global scale when trait-climate relationships characterized in this study are explicitly implemented.
In parallel, relationships highlighted in this study may help to develop or validate new methods to simulate plant acclimation. Used in a prognostic way, this approach could enable to study correlations at the canopy scale and to assess the behavior of trait-related parameters that are difficult to observe experimentally.

Several known ecological properties, observed at the site/leaf scale, emerged from model-data assimilation. However, quantitative comparisons with observations were possible only for two of them, $SLA$ and $Lage$, which are also the two most studied traits. This is mainly because TBMs use model-specific parameters that cannot be directly compared to standard trait observations, but also because concomitant observations of functional traits, both in space and time, are scarce in the literature. A recommendation to the TBM community would be to make use of parameters (and processes) that can be related directly to observations in order to unit vegetation model and functional traits (for instance the use of the Specific Root Length for belowground processes).

We argue that co-located systematic and standardized trait observations (starting with key traits related to phenology -$SLA$, $LAI$-, photosynthesis -$Vcmax$, $Jmax$, $Topt$-, water transport -$gs$- and allocation -$Carbon: Nitrogen ratio$, $shoot/root$; (Law et al., 2008) along with biometric data are needed at the FLUXNET sites or within other environmental observation networks such as ICOS (Integrated Carbon Observation System) or NEON (National Ecological Observatory Network) if we seek to distinguish temporal and spatial components of trait variability across biomes and climates. The creation of a FLUXNET trait database could improve our comprehension of trait acclimation and help us to disentangle the differences observed at regional and local scales, to improve the up-scaling of processes from the leaf to the canopy/ecosystem level and to properly calibrate/validate ecosystem models.
Supporting information

Appendix S1: Description of PFTs, model parameters and equations
- Table S1.1: List of plant functional types.
- Table S1.2: List of main equations involving optimized parameters.
- Table S1.3: Default parameter value and range allowed by the optimization algorithm.

Appendix S2: List of FLUXNET sites used for the analyses (xlsx file).

Appendix S3: Optimization performances
- Figure S3.1: Distribution of optimized parameter values.
- Table S3.4: Mean $a priori$ and $a posteriori$ RMSE between observations and simulations.
- Table S3.5: Mean parameter uncertainty reduction between prior and posterior simulations.

Appendix S4: Relationships between traits
- Figure S4.2: Correlation matrices between traits optimized against site-year GPP.
- Figure S4.3: Correlation matrices between traits optimized against site GPP.
- Table S4.6: Extended Table 3 with all relationships.

Appendix S5: Relationships between traits and climate
- Figure S5.4: Correlation matrices between traits and environmental variables optimized against site-year GPP.
- Figure S5.5: Correlation matrices between traits and environmental variables optimized against site GPP.
- Table S5.7: Extended Table 4 with all relationships.

Data accessibility

All FluxNet data can be downloaded at: https://fluxnet.fluxdata.org
Information about the ORCHIDEE model, source code and contact: http://orchidee.ipsl.fr/
Information about the data assimilation system ORCHIDAS: https://orchidas.lsce.ipsl.fr/
References


Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain


Table 1: Description of the 14 optimized parameters and associated processes. All the parameters are common to each PFT. Kbm and bbdate are scaling factor added in the model to improve the optimization of the seasonal cycle of the GPP but are not analyzed in the study. (See Table S1.2; Appendix 1 for the detailed equations involving each parameter).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Processes involved</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLA</td>
<td>Specific leaf area (m² gC⁻¹)</td>
<td>Photosynthesis, Phenology, Allocation</td>
</tr>
<tr>
<td>Lage</td>
<td>Leaf lifespan (days)</td>
<td>Photosynthesis, Phenology</td>
</tr>
<tr>
<td>Vcmax</td>
<td>Maximal carboxylation rate limited by CO₂ (µmol m² s⁻¹)</td>
<td>Photosynthesis</td>
</tr>
<tr>
<td>Vj/Vc</td>
<td>Ratio between the maximal carboxylation rate limited by light and Vcmax</td>
<td>Photosynthesis</td>
</tr>
<tr>
<td>Topt</td>
<td>Optimal temperature of the photosynthesis (°C)</td>
<td>Photosynthesis</td>
</tr>
<tr>
<td>gslope</td>
<td>Slope of the Ball-Berry relationship for the stomatal conductance</td>
<td>Photosynthesis, energy budget</td>
</tr>
<tr>
<td>LAImax</td>
<td>Maximal leaf area index</td>
<td>Photosynthesis, Phenology, Allocation</td>
</tr>
<tr>
<td>Klai</td>
<td>Minimal fraction of LAImax for the use of carbohydrate reserves</td>
<td>Allocation</td>
</tr>
<tr>
<td>bbdate</td>
<td>Budburst date (day of the year)</td>
<td>Phenology</td>
</tr>
<tr>
<td>tauleaf</td>
<td>Period after budburst during which the use of carbohydrates is allowed</td>
<td>Allocation</td>
</tr>
<tr>
<td>Csenes</td>
<td>Temperature for leaf senescence (used only for deciduous)</td>
<td>Phenology</td>
</tr>
<tr>
<td>Kbm</td>
<td>Multiplicative factor for the initial leaf biomass (used only for evergreens)</td>
<td>Phenology, Allocation</td>
</tr>
<tr>
<td>Kroot</td>
<td>Exponential factor describing the root profile and depth</td>
<td>Water budget, Photosynthesis</td>
</tr>
<tr>
<td>Wlim</td>
<td>Minimal threshold at which the photosynthesis becomes limited by water availability</td>
<td>Photosynthesis</td>
</tr>
</tbody>
</table>
Table 2: Description of bio-climatic variables calculated at each site and for each year.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAT</td>
<td>Latitude</td>
<td>°N</td>
</tr>
<tr>
<td>MAT</td>
<td>Mean annual temperature</td>
<td>Celsius</td>
</tr>
<tr>
<td>TMAX</td>
<td>Mean temperature of the warmest month of the year</td>
<td>Celsius</td>
</tr>
<tr>
<td>TMIN</td>
<td>Mean temperature of the coldest month of the year</td>
<td>Celsius</td>
</tr>
<tr>
<td>TVAR</td>
<td>Temperature difference between TMAX and TMIN</td>
<td>Celsius</td>
</tr>
<tr>
<td>DTR</td>
<td>Yearly average of diurnal temperature range</td>
<td>Celsius</td>
</tr>
<tr>
<td>MAP</td>
<td>Mean annual precipitation</td>
<td>mm y(^{-1})</td>
</tr>
<tr>
<td>REH</td>
<td>Mean annual relative humidity</td>
<td>%</td>
</tr>
<tr>
<td>SW</td>
<td>Mean annual downward shortwaves radiation (visible and near IR)</td>
<td>W m(^{-2})</td>
</tr>
<tr>
<td>PDRY</td>
<td>The driest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.</td>
<td>mm y(^{-1})</td>
</tr>
<tr>
<td>RELP</td>
<td>PDRY divided by MAP</td>
<td>fraction</td>
</tr>
<tr>
<td>SHUM</td>
<td>Yearly averaged soil humidity</td>
<td>fraction</td>
</tr>
<tr>
<td>GSL</td>
<td>MATgs, DTRgs, SWgs, MAPgs, REHgs and SHUMgs are the same variables averaged during the growing season of the plant</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3: Relationships between trait-related parameters. For some relationships, values are log-transformed (x). For each relationship is the number of sites, as well as the correlation coefficient (r, blue when negative; red when positive). Only relationships with an absolute and significant (p-value<0.05) correlation coefficient higher than 0.5 are listed for the different groups of PFT: all, broadleaves (bro; TroEB, TemEB, TDB, BDB), needleleaves (need; TEN, BEN), evergreens (ever; TroEB, TemEB, TEN, BEN), deciduous (dec; TDB, BDB) and C3 grasses (gra). Note that evergreens include needleleaves and that broadleaves include deciduous. The type of relationship is given for each trait: 0= verified with ecological observations; 1=partially verified on similar data or 3= different from observations. When available, the reference for verification is given. Well constrained parameters are in bold, parameters with a risk of equifinality are normal, poorly constrained parameters are in italics. Refer to Table 1 for the description of each parameter.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>r</th>
<th>PFT</th>
<th>log</th>
<th>SMA slope</th>
<th>n sites</th>
<th>references</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lage SLA</td>
<td>-0.67</td>
<td>ever</td>
<td>x</td>
<td>-1.39</td>
<td>49</td>
<td>(Reich et al., 1999); (Wright et al., 2004)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>-0.53</td>
<td>bro</td>
<td>x</td>
<td>-3.47</td>
<td>37</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>-0.63</td>
<td>All</td>
<td>x</td>
<td>-1.92</td>
<td>98</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Lage Vcmax</td>
<td>-0.90</td>
<td>Bro</td>
<td>x</td>
<td>-1.69</td>
<td>37</td>
<td>(Xu et al., 2017)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>-0.65</td>
<td>Dec</td>
<td>x</td>
<td>-2.15</td>
<td>23</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>-0.59</td>
<td>All</td>
<td>x</td>
<td>-3.13</td>
<td>98</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>gslope Lage</td>
<td>-0.70</td>
<td>Bro</td>
<td>x</td>
<td>-0.74</td>
<td>37</td>
<td>(Reich et al., 1992); (Poorter &amp; Bongers, 2006)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>-0.57</td>
<td>Grass</td>
<td>x</td>
<td>0.00</td>
<td>26</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>gslope SLA</td>
<td>-0.62</td>
<td>Ever</td>
<td>x</td>
<td>-534.01</td>
<td>49</td>
<td>(Poorter &amp; Bongers, 2006)</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>-0.52</td>
<td>Dec</td>
<td>x</td>
<td>418.99</td>
<td>23</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>-0.51</td>
<td>Grass</td>
<td>x</td>
<td>-235.65</td>
<td>26</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>LAImax SLA</td>
<td>0.60</td>
<td>Need</td>
<td></td>
<td>422.11</td>
<td>35</td>
<td>(Pierce et al., 1994)</td>
<td>1</td>
</tr>
<tr>
<td>SLA Vcmax</td>
<td>-0.55</td>
<td>Ever</td>
<td>x</td>
<td>-1.28</td>
<td>49</td>
<td>(Niinemets et al., 2007)</td>
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</tr>
<tr>
<td></td>
<td>-0.53</td>
<td>Need</td>
<td>x</td>
<td>-0.75</td>
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<td>gslope Wlm</td>
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<td>Bro</td>
<td>x</td>
<td>1.61</td>
<td>37</td>
<td>(Lin et al., 2015)</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>0.52</td>
<td>Ever</td>
<td>x</td>
<td>1.47</td>
<td>49</td>
<td></td>
<td>3</td>
</tr>
</tbody>
</table>
Table 4: Relationships between trait-related parameters and climate variables. For some relationships, traits values are log-transformed (x). For each relationship is given the correlation coefficient (r). Only relationships with an absolute (and significant p-value<0.05) correlation coefficient higher than 0.5 are listed for the different groups of PFT: all, broadleaves (bro; TroEB, TemEB, TDB, BDB), needleleaves (need; TEN, BEN), evergreens (ever; TroEB, TemEB, TEN, BEN), deciduous (dec; TDB, BDB) and C3 grasses (gra). The type of relationship is given for each trait: 0= verified with ecological observations; 1= partially verified on similar data; 2= not verified or, 3= different from observations. When available, the reference for verification is given. Well constrained parameters are in bold, parameters with a risk of equifinality are normal. Refers to Table 1 and 2 for the description of each parameter and climate variables respectively.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Climat</th>
<th>r</th>
<th>PFT</th>
<th>log SMA slope</th>
<th>Référence</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAT</td>
<td>0.59</td>
<td>ever</td>
<td>24.90</td>
<td>(Reich et al., 2014)</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.56</td>
<td>bro</td>
<td>-13.44</td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MAP</td>
<td>0.66</td>
<td>grass</td>
<td>1.14</td>
<td>(van Ommen Kloeke et al., 2012)</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.65</td>
<td>need</td>
<td>x -0.66</td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MAT</td>
<td>-0.78</td>
<td>ever</td>
<td>x -16.95</td>
<td>(Wright et al., 2005; van Ommen Kloeke et al., 2012; Reich et al., 2014)</td>
<td>0</td>
<td></td>
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<tr>
<td></td>
<td>-0.62</td>
<td>need</td>
<td>x -17.93</td>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0.54</td>
<td>grass</td>
<td>x 107.81</td>
<td></td>
<td>-</td>
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<tr>
<td></td>
<td>0.53</td>
<td>bro</td>
<td>x 30.14</td>
<td></td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>SW</td>
<td>-0.53</td>
<td>ever</td>
<td>x -1.84</td>
<td>(Poorter &amp; Bongers, 2006)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.52</td>
<td>bro</td>
<td>x 3.85</td>
<td></td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>TMIN</td>
<td>-0.65</td>
<td>ever</td>
<td>x -30.99</td>
<td>(Wright et al., 2005; van Ommen Kloeke et al., 2012; Reich et al., 2014)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>MAP</td>
<td>0.54</td>
<td>need</td>
<td>x 0.37</td>
<td>(Wright et al., 2005)</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>MAPgs</td>
<td>0.57</td>
<td>ever</td>
<td>x 0.47</td>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>MAT</td>
<td>0.65</td>
<td>ever</td>
<td>x 12.16</td>
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<td>MATgs</td>
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<td>x -0.86</td>
<td>(Wright et al., 2005)</td>
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<tr>
<td></td>
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<td>dec</td>
<td>x -0.96</td>
<td></td>
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<tr>
<td>RELP</td>
<td>0.60</td>
<td>dec</td>
<td>x 0.25</td>
<td></td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>0.59</td>
<td>bro</td>
<td>x 0.08</td>
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<td>-</td>
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</tr>
<tr>
<td>SW</td>
<td>0.53</td>
<td>ever</td>
<td>x 0.00</td>
<td>(Givnish et al., 2004; Poorter &amp; Bongers, 2006; Reich et al., 2014)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>MAP</td>
<td>-0.59</td>
<td>grass</td>
<td>x -1.12</td>
<td></td>
<td>-</td>
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<tr>
<td>PDRY</td>
<td>0.58</td>
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<td>0.02</td>
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<td>1</td>
</tr>
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<td>REH</td>
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<td>19.24</td>
<td></td>
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<td>1</td>
</tr>
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<td>0.66</td>
<td>bro</td>
<td>42.67</td>
<td>(Lin et al., 2015)</td>
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<td>dec</td>
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<td>SHUMgs</td>
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</tr>
<tr>
<td>SWgs</td>
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<td>dec</td>
<td>-0.08</td>
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<td>-</td>
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</tr>
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<td>Vcmax</td>
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<td>bro</td>
<td>-4.77</td>
<td>(Ali et al., 2015)</td>
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<tr>
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<td>bro</td>
<td>-1.15</td>
<td>(Ali et al., 2015)</td>
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gslope
Figure 1: Schematic representation of the modeling protocol followed in this study. For each FLUXNET site-year (blue), the model ORCHIDEE (green) was calibrated with the data assimilation system ORCHIDAS (red) in order to reproduce GPP observations. The ORCHIDAS system uses a gradient-based approach (L-BFGS-B) to reduce the cost function $J(x)$. For each site-year, 14 parameters (listed in Table 1) were optimized 10 times with different initial values. The best calibration, i.e. leading to the minimum value of $J(x)$, was retained. This procedure was repeated for each site-year, resulting in 371 sets of 14 independently optimized parameters. Finally, correlations between optimized parameters and climate were explored using standardized major axis regressions.
Figure 2: Error correlation between optimized parameters (derived from the A matrix) averaged over deciduous trees, evergreen trees, and C3 grass. The color scale gives the error correlation coefficient. For more clarity, the coefficient is indicated in % in each matrix cell. The description of each parameter is listed in Table 1.
Figure 3: Four examples of co-variations obtained between optimized parameters (Table 1) and environmental conditions (Table 2) of the sites for PFTs TroEB (black square), TEN (red square), TemEB (green triangle), TDB (blue square), BEN (cyan dots) and BDB (pink dots). Each point represents the mean optimized parameter (environmental variable) value for one site while the error bars represent the inter-annual variability (no bars means only one year of measurement). The red line represents the slope of the standardized major axis regression.