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**A new approach for optimal discretization of plant functional types in a
process-based ecosystem model with forest management: a case study of
temperate conifers.**

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ABSTRACT

Aim

Dynamic global vegetation models (DGVM) use a discretization of forest vegetation based on plant functional types (PFT). The physiological and ecological parameters used to model a given PFT are usually fixed, being defined from point-based observations while model applications are often grid-based. This rigid approach is causing spatial biases in the results of DGVM-simulated productivity and biomass-related variables. We aim to overcome this limitation with a new approach that uses a hierarchical classification of forest PFT parameters from traits retrieved from the literature and from the TRY global database of plant traits. This approach is applied to temperate conifers in the DGVM ORCHIDEE-FM, which has previously been shown to produce systematic biases in the simulation of biomass and biomass increments.

Location

Temperate coniferous forests; France

Time period

2005-2012

Major taxa studied

Gymnosperms

Methods

The five major coniferous species in France, *Abies alba*, *Picea abies*, *Pinus pinaster*, *Pinus sylvestris* and *Pseudotsuga menziesii*, were grouped objectively into PFTs within the ORCHIDEE-FM DGVM using a hierarchical classification based on 12 key attributes related to photosynthesis, phenology and allometric relationships.

52 **Results**

53 We show that the single PFT covering all temperate coniferous forest that was used by default
54 in ORCHIDEE-FM could be replaced by two representative sub-categories defined by grouping
55 species-level data, without necessarily having to adopt a set of parameters for each species. The
56 definition of new temperate conifer PFTs with this approach allows us to reduce the spatial
57 heterogeneity by 40% in average in model-measurement misfit for stand volume, growth and
58 stand density at the regional scale.

59 **Main conclusions**

60 The proposed approach to improve the representation of plant functional types in DGVMs,
61 while keeping the number of different PFTs manageable, is promising for application to regions
62 where a single PFT can correspond to a number of different species.

INTRODUCTION

Dynamic global vegetation models (DGVMs) simulate the biogeochemical and hydrological processes involved in ecosystem functioning. They model the controls on the fluxes of carbon, energy and water from local up to regional and global scale. DGVMs also simulate the response of processes and state variables to environmental drivers. Most of these models use a discretized representation of vegetation using Plant Functional Types (PFT), with generally a dozen different PFTs representing the world's vegetation. By definition, each PFT represents a “mean” type of vegetation defined by a set of traits (translated to model parameters). While the use of a limited number of PFTs is practical for grid-based simulations at large scale, this rather rigid representation of the vegetation does not allow a robust analysis of regional gradients in productivity and biomass, and leads to over-simplify processes controlling vegetation dynamics. It is therefore a source of uncertainty in model predictions (Alton, 2011).

The research question of how to deal with the uncertainties resulting from the discrete and rigid representation of PFTs in DGVMs has been addressed by increasing the number of PFTs, or by introducing a continuous spatial variation of vegetation parameters, e.g. using plant trait datasets (Kleidon & Mooney, 2000; Reu *et al.*, 2011; Van Bodegom *et al.*, 2012; Wullschleger *et al.*, 2014; Verheijen *et al.*, 2015). A continuous parameterization of parameters allows spatial variability of parameters within a given PFT (Van Bodegom *et al.*, 2012; Pavlick *et al.*, 2012; Verheijen *et al.*, 2013). However, this method needs a large amount of data for model calibration. Although plant trait databases are building up an increasingly large bank of relevant data, the quality and spatial representativeness of these data might not yet be sufficient to derive robust relationships at the global scale, and even less so at regional scale, such as in our case for temperate coniferous forest in Europe.

In this context, increasing the number of PFTs seems a reasonable compromise. Naudt *et al.* (2015) defined one PFT by dominant European tree species. This strategy is relevant for forests

88 in Europe where only a few dominant tree species prevail, but it is impractical in higher
89 biodiversity systems such as grasslands or tropical forests, in which intermediate levels of PFT
90 representation are needed.

91 Past studies mostly focused on biogeographical or climatic envelopes to define new PFTs for
92 DGVMs (Nemani & Running, 1996; Bonan *et al.*, 2002; Harrison *et al.*, 2010) and often sought
93 to find an optimal and/or minimal subset of traits to give the best classification (Pillar, 1999;
94 Pausas & Lavorel, 2003; Pillar & Sosinski, 2003; Bernhardt-Römermann *et al.*, 2008).
95 Boulangeat *et al.* (2012) already argued for the necessity to improve PFTs in DGVMs by
96 regrouping representative species with a classification based on key biological characteristics.

97 Here, we propose an approach to refine the PFT representation in typical DGVMs through the
98 case study of improving the representation of the spatial variability of the parameters of the
99 PFT “temperate needleleaf forest” (TNF) across Europe, using the ORCHIDEE-FM DGVM.

100 The ORCHIDEE-FM DGVM (“ORganising Carbon and Hydrology In Dynamic Ecosystems –
101 Forest Management”; Krinner *et al.*, 2005; Bellassen *et al.*, 2010) simulates the growth, and the
102 competition between individuals leading to density-driven mortality within a forest stand, and
103 optionally an idealized management practice of plantation forests, assumed to be even-aged.

104 The results from this DGVM was evaluated for temperate broadleaf and needleleaf forest in
105 Europe against, among other data sources, biometric data obtained from numerous plots from
106 national forest inventories by Bellassen *et al.*, (2011). Although simulations of biomass and
107 growth were satisfactory for broadleaf forests at the regional scale, the model was not able to
108 reproduce regional patterns for temperate needleleaf forests. Bellassen *et al.* (2011) found
109 regional biases in conifer forests standing volume and growth as a function of forest age, which
110 could not be corrected by simply optimizing parameters, unlike for broadleaf forests
111 (Supplementary Fig.S1). They concluded that the main reason for this model systematic error
112 was the use of a unique conifer PFT associated with a single set of parameters. This suggests

that the model suffers more weakness due to its too coarse discretization of vegetation, than from its internal structure and parameter values.

Therefore, in this study, we seek to establish if TNF species can be objectively sub-divided into sub-groups with coherent set of parameters for inclusion in the ORCHIDEE FM DGVM. We search for coherent parameters related to eco-physiological attributes, namely photosynthesis, phenology, allometry and differences in management practice.

METHODS

We proposed a new approach for improving the representation of PFTs in ORCHIDEE-FM based on literature review and field data analysis. This method combines three steps:

1) We first identified 12 key *sensitive* eco-physiological parameters, i.e., parameters that have important influence on the model output. These parameters can be related to photosynthesis, phenology, allometry and management parameters for TNF forests. The definition of *sensitive* is based on previous work that optimized parameters against net ecosystem exchange (NEE) CO₂ and evaporation flux measurements at TNF sites with eddy-covariance technique.

2) Next, we retrieved a range of values for each sensitive parameter obtained in step-1, based on a literature review and the TRY global trait database (Kattge *et al.*, 2011). This search was restricted to the five most abundant TNF species present in France (Vallet *et al.*, 2006): Silver fir (*Abies alba*), Norway spruce (*Picea abies*), Maritime pine (*Pinus pinaster*), Scots pine (*Pinus sylvestris*) and Douglas fir (*Pseudotsuga menziesii*).

3) Based on the results of 1) and 2), we showed that TNF species can be objectively regrouped using a hierarchical classification into two homogeneous clusters that have parameter similarities. Implemented in the ORCHIDEE model, we showed that the new

PFTs improve the spatial representation of conifer stands. The consistency between PFTs based on parameter values from the literature and PFTs used by ORCHIDEE was assessed by comparing the parameter values of each cluster defined with independent photosynthesis and phenological data from the literature to the values obtained from the calibration of ORCHIDEE using eddy covariance (EC) evaporation and NEE measurements (Santaren *et al.*, 2007; Kuppel *et al.*, 2014).

Description of the ORCHIDEE-FM model

ORCHIDEE is a process-based vegetation model that can be run point-based or grid-based (Krinner *et al.*, 2005). In the standard version of ORCHIDEE (v.1.9.6) an average forest is simulated as a mature stand in near equilibrium between growth and mortality. For given vegetation, soil type and climatic condition, ORCHIDEE simulates the carbon, water and energy budgets on a half-hourly time step (Fig. 1).

Bellassen *et al.* (2010) added a forest management module (FM; Fig. 1) to ORCHIDEE (v.1.9.6) to simulate self-thinning and management. The FM module replaces an “average tree” representation with a statistically distributed population of individual trees and includes rules for both natural mortality and human interventions. This forest management version of the model is called ORCHIDEE-FM (v.1.9.6-rev.30). It simulates carbon stocks and detailed stand structure of forests of varying ages (Bellassen *et al.*, 2011) which can be directly compared with forest inventory data or ecological site biometric observations. The FM equations are fully described by Bellassen *et al.* (2010).

Selection of *sensitive* eco-physiological parameters

The starting point for improving the description of TNF forests is the determination of the variability of so called sensitive or influential eco-physiological parameters among the TNF

species. Among all the parameters of ORCHIDEE-FM, we defined as influential those whose variations have a significant effect on the modelled stand biomass. The selection of influential parameters was carried out by comparing information from previous sensitivity tests made by Bellassen *et al.* (2010) to the results of an optimization of ORCHIDEE eco-physiological parameters made by Kuppel (2012) using eddy-covariance measurements. Both methods allow the identification of sensitive parameters, given different “target” state variables. Bellassen *et al.* (2010) identified “slow” parameters that control stand density and biomass dynamics on time scales of decades (hereafter B-parameters), while Kuppel (2012) identified mainly “fast” parameters that control physiological processes controlling fluxes (hereafter P-parameters), on time scales of days to seasons. Both fast and slow parameters interact with each other in determining ecosystem carbon state variables in the model equations (Fig. 1). This interaction is non-symmetrical, however. Slow parameters controlling long-term forest growth and carbon stocks have a small impact on hourly to seasonal fluxes, whereas fast parameters do influence decadal net primary productivity (NPP) and thus a change from their default value is expected to modify the decadal stand-scale growth, competition and mortality, and thus the long-term changes of biomass.

The method used to select each parameter is fully described in Appendix S2 (see Table 1 for parameters names). The results are summarized here. Three B-parameters were selected as being influential: allometric coefficients that govern the tree biomass-to-circumference ratios (b_{bc}), self-thinning parameters ($\ln(\alpha_{st})$ and β_{st}) and the threshold of stand density at which forest management thinning is set to occur (rdi_target) for managed forests. Six P-parameters were found influential: the maximum leaf-level limited carboxylation rate normalized at 25°C (V_{cmax_opt}), the optimal temperature for photosynthesis (T_{opt}), the slope of the Ball-Berry linear relationship between stomatal conductance (g_{slope}) and net assimilation rate, the specific leaf area (SLA) and the critical leaf age for leaf senescence ($L_{age,crit}$).

Processes in which the different parameters identified in this study are involved are illustrated in Fig. 1 and listed in Table 1. The default values of these parameters for the TNF PFT in ORCHIDEE are as defined by Krinner *et al.* (2005) and by Bellassen *et al.* (2010) and listed in Table 2. Optimized values obtained from inversion of the fast parameters against EC measurements are from Santaren *et al.* (2007) and Kuppel *et al.* (2014).

Literature review of key parameters

We gathered species-specific data for the values of each sensitive parameter listed in Table 1. A search of the literature (up to 2012) was conducted for the predominant TNF species found in France. In addition of this literature search, a number of values were obtained through the TRY database (Kattge *et al.*, 2011), especially for *SLA*. The number of values found for each parameter is indicated in Fig. 2 and Table 2. The literature was first searched for each species and each parameter; the search was then restricted to temperate regions (Köppen classification; Peel *et al.*, 2007). TRY values that were also in the literature were eliminated to avoid duplication; and when multiple measurements were available at a given site, the median value of the reported values was used. Care was taken to ensure the physiological meaning of the data found in the TRY database corresponded to the model parameter definitions. The use of mean values reduced the size of the dataset and prevented any bias from over-sampling a few better-measured sites.

For all parameters identified as influential, we tried to minimize the uncertainty due to different measurement methods by filtering or correcting data whenever possible. Values were not corrected according to environmental variability, nor species provenance or age. All references were searched for each parameter described in the following sections and a detailed description of the methodology used to homogenize values for each parameter can be found in Appendices B and C in the Supporting Information.

Even though it is a *sensitive* parameter according to Kuppel *et al.* (2012), the number of data reviewed for g_{slope} was insufficient to perform a separate analysis per species within the TNF PFT (Fig. 2). We thus decided to extract another parameter from the literature, the maximal stomatal conductance (g_{smax} – even though it is not directly used in ORCHIDEE). We defined g_{smax} as the maximum conductance measured at one site at any measurement period. The model is sensitive to the value of g_{slope} , but because we have no evidence that g_{smax} is also a key parameter, the following analyses were performed either including or excluding g_{smax} .

216

217 **Clustering of species based on parameters values**

For all parameters, except rdi_target , T_{opt} (see Table 1 for definitions) and g_{slope} , because of insufficient data, the inter-species and intra-species parameter variabilities were calculated using Kruskal–Wallis one-way analysis of variance and the Mahalanobis distance (distance between species taking into account the parameter variance; Mahalanobis, 1936):

$$D(x) = \sqrt{(x - \mu)^T \sum^{-1} (x - \mu)} \quad (1)$$

where x is a vector of data (here different parameters) with p columns, μ the mean of the distribution of length p , \sum the covariance matrix ($p \times p$) of the distribution. These methods have the advantage of providing a statistical test of similarity. Their drawback is the impossibility of obtaining a unique set of species clusters based on the variability of all the parameters.

As all parameters are quantitative, we used a clustering algorithm to objectively define homogeneous groups of species based on Ward's method (1963). In this method, all parameter median values are centred and scaled to calculate dissimilarity (distance, eq.2).

$$D(C_1, C_2) = \sqrt{\frac{n_1 n_2}{n_1 + n_2}} d(\mu_1, \mu_2) \quad (2)$$

Where $D(C_1, C_2)$ is the distance between clusters C_1 and C_2 , n_1 and n_2 the number of data, and $d(\mu_1, \mu_2)$ the distance between their respective centroids.

Data treatment was entirely performed with R software (R Team 2011).

ORCHIDEE-FM Simulations

First, we analysed previous regional simulations from Bellassen *et al.* (2011) in the light of the new PFT classification by comparing model/measurement errors from Bellassen *et al.*, (2011) to the distribution of the newly defined PFTs.

In addition, four sets of simulations were performed to assess the gain (or loss) of information obtained by different sub-divisions of TNF species, each based on coherent parameter values. The first set (REF) uses the default parameter values and processes of ORCHIDEE-FM as described by Bellassen *et al.* (2010), that is parameters are the same for all TNF forests. The second configuration (S1) use one PFT to represent TNF forest but this PFT is parameterized according to results of the literature review. The third set (S2) was performed using the new PFTs corresponding to species groups obtained from the hierarchical clustering of parameters. The fourth simulation (S3) was performed with the parameters of each TNF species (5 in total), each species being modeled as a separate PFT. All the simulations are evaluated against the French NFI observations interpolated at a 0.25° spatial resolution. We simulated 50 years old stands. To minimize bias between simulations and observations, we averaged the simulation outputs over a 10 year period (between years 45 and 55) and only trees with a diameter higher than 7.5 cm were used.

The same protocol and pedo-climatic inputs as in Bellassen *et al.* (2011) were used for all the simulations. No historical change in species distribution or forest area was taken into account

in the simulations. The performance of each simulation was assessed against observations by using the Spearman's rank correlation coefficient for three different variables: the average stand aboveground volume, volume increment and stand density.

RESULTS

Synthesis of parameter values

We found differences in the quantity of data collected for the different parameters. For instance, 336 values were collected for *SLA* while only one value per species could be obtained for T_{opt} and *rdi_target* (Table 3). There is also a range in the number of data available per species. The values for *Pinus sylvestris* and *Picea abies* are more numerous than for *Abies alba*, *Pinus pinaster* and *Pseudotsuga menziesii* in particular for V_{cmax} , *SLA* and g_{smax} . The mean coefficient of variation (CV) for parameters V_{cmax} , *SLA* and g_{smax} are relatively high (0.35, 0.43 and 0.71, respectively). This spread of parameter distributions could be the result of environmental conditions, bias in measurement method or representation.

Differences between species

Species was found to be a statistically significant explanatory variable for differences in P-parameters. According to the Kruskal-Wallis one-way analysis of variance, the values of V_{cmax25} , J_{max}/V_{cmax} , $L_{age,crit}$ and *SLA* were found to be significantly different between species (p-value<0.05). Variance analysis shows a significant inter-species variability for most P-parameters, whereas B-parameter differences are statistically not significant between species. For parameters V_{cmax} , J_{max}/V_{cmax} , *SLA* and *Longevity*, the Mahalanobis distance between species is found to be higher than for g_{smax} (Fig.S2 in Appendix S1). However for B-parameters, the distance between species is relatively lower than for P-parameters. All *Pinus* species fall into

the same group for P-parameters, which supports grouping these species into one group for modelling carbon stocks and fluxes.

Differences in parameters between literature values and eddy covariance optimized values

We observe discrepancies between literature values and values optimized from eddy covariance data for several parameters. V_{cmax25} values observed in the literature for *Pinus pinaster* and *Pinus sylvestris* (90.31 and 106.61 $\mu\text{mol m}^{-2} \text{s}^{-1}$) are higher than optimized values obtained by Kuppel *et al.* (2014) from 20 conifer sites (viz., 41.7 and 31.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Table 3). By contrast, for non-pine species, V_{cmax25} estimated from literature data (at leaf scale) are found to be within the range of the results from Kuppel *et al.* (2014). For T_{opt} , only values obtained for *Pinus sylvestris* are close to the values optimized by Kuppel *et al.* (2014), but the median value considering all TNF species is twofold higher in the literature data than in Kuppel *et al.* (2014) (32.3°C compared to 17.5°C). SLA literature values are half those of Kuppel *et al.* (2014) (10 $\text{mm}^2 \text{mg}^{-1}$), excepted for *Pseudotsuga menziesii* for which we found an SLA of 7.08 $\text{mm}^2 \text{mg}^{-1}$. For $L_{age,crit}$, only the literature value for *Pinus sylvestris* (34.0 months) is close to Kuppel *et al.* (2014) (35.6 months). Too few data were available to compare g_{slope} for all species, however the single literature value reviewed for *Pinus pinaster* (10.05) is in the range of the inversion results of Kuppel *et al.* (2014) (8.8) and Santaren *et al.* (2007) (8.1). The values of g_{slope} obtained from the literature for *Picea abies* (5.94) and *Pinus sylvestris* (5.59) are smaller than values found by the Bayesian calibration of Kuppel *et al.* (2014). Results from the Santaren *et al.* (2007) and Kuppel *et al.* (2014) optimizations are summarized in Table 3.

Differences between literature and values derived from forest inventory data for

B-parameters

In addition to the literature search, B-parameters linked to biomass dynamics (b_{bc} , $\ln(\alpha_{st})$ and β_{st}) were re-determined by fitting to the French national forest inventory (NFI) data (IFN, 2012; refer to Appendix S2 for a complete description). Fitted values of b_{bc} are from this study, while values of $\ln(\alpha_{st})$ and β_{st} are from Charru *et al.* (2012) (also obtained from French NFI). For these three B-parameters, most of the values fitted using the French NFI data were found to be out of the range of the literature values (blue dots in Fig. 2). Values for b_{bc} and β_{st} are larger for *Pinus* compared to literature values, but the opposite is found for $\ln(\alpha_{st})$. For *Picea abies*, values of b_{bc} and β_{st} are smaller than literature values and larger for $\ln(\alpha_{st})$. Exceptions are *Pseudotsuga menziesii* for which $\ln(\alpha_{st})$, β_{st} and b_{bc} are in the same range between the two approaches, and *Abies alba* for parameters $\ln(\alpha_{st})$ and β_{st} .

Species clustering

The first clustering of species, based on all parameters, is called global classification (Fig. 3a). It results in a first group composed of *Abies alba*, *Picea abies* and *Pseudotsuga menziesii* and a second group with *Pinus sylvestris* and *Pinus pinaster*. Two potential biases were tested for: 1) parameter redundancy – the inclusion of different parameters related to the same eco-physiological process may give too much weight to this process in the classification – and 2) the type of parameter used for the classification, because P- and B-parameters are related to different processes and may have uneven weights in the classification. To test for these possible biases, three other classifications were performed. A classification based on P-parameters only was found to be equivalent to the global classification, yet with a reduced distance between groups and a longer distance between *Pseudotsuga menziesii* and *Picea abies*, *Abies alba* (Fig. 3b). Another classification based on B-parameters resulted in grouping of *Pseudotsuga*

319 *menziesii* and *Picea abies* on one side, *Pinus sylvestris*, *Abies alba* and *Pinus pinaster* on the
320 other side (Fig. 3c).

321 To decrease redundancy, a second classification was based on all parameters except $\ln(\alpha_{st})$, T_{optj}
322 and J_{max}/V_{max} to minimize redundancy of these parameters with β_{st} , T_{optv} and V_{cmax25} respectively
323 (Figs 3d and 3e). The two main clusters of this second classification are found to be the same
324 as in the (first) global classification, and appear even more clearly since the distances between
325 species within each cluster are relatively smaller than in the global classification. If we separate
326 again between the reduced parameter set for the P- and B-parameters (hereafter rP and rB), the
327 classification result using rB-parameters only is equivalent to the one using rP-parameters only.
328 From this we conclude that two new PFTs describing temperate conifers can be defined, namely
329 PFT1 with *Abies alba*/*Picea abies*/*Pseudotsuga menziesii* and PFT2 with *Pinus pinaster*/*Pinus*
330 *sylvestris*.

331 **Model evaluation**

332 We reprocessed the results of Bellassen *et al.* (2011) with the new classification. The spatial
333 distribution of the new PFTs within the TNF group is illustrated in the Supplementary
334 Information (Fig. S3). It allows us to explain qualitatively the spatial distribution of differences
335 between observed and simulated volumes and volume increments (Fig. 4). From the
336 observations available in the French NFI dataset we separated pixels where only one PFT was
337 present from pixels where the two PFTs coexist. Pixels which show an overestimation of the
338 volume increment correspond to a predominance of PFT2 (Fig. 4a); and the opposite, pixels
339 showing an underestimation of the volume increment correspond to a predominance of PFT1.
340 This distinction is also visible on pixels where the two PFTs are present (Fig. 4b).

341 Figure 5 illustrates the spatial correlation between observed and simulated volume, volume
342 increment and stand density with 1, 2 or 5 PFTs. Considering TNF as a single PFT with

parameters values retrieved from the literature (S1) degrades the spatial representation of volume and volume increment compared to the reference simulation (REF). Increasing the number of PFTs improves the spatial correlation (r) between observed and simulated total aboveground volume ($r_{REF}=0.27$, $r_{S2}=0.73$), volume increment ($r_{REF}=0.44$, $r_{S2}=0.56$) and average stand density ($r_{REF}=-0.16$, $r_{S2}=0.61$). However, further increasing the number of PFTs up to one PFT per species in S3 does not improve the results compared to S2, excepted for the volume increment ($r_{S2}=0.56$, $r_{S3}=0.7$).

DISCUSSION

The species clustering method

The main result of this study is that the temperate coniferous species planted in French forests can be grouped into a few distinct PFTs from our clustering analysis method based on *sensitive* parameter similarity (Fig.3). The use of a reduced set of influential parameters, designed to prevent redundancy of information across parameters, leads to a similar grouping of species when considering either P- or B-parameters, or both, to group species. This suggests that the parameter classification method proposed here can determine groups of species. The significant inter-species variability observed for most P-parameters, but not for B-parameters could be partly explained by the fact that some B-parameters related to forestry (allometric parameters or *rdi*) are determined from managed stand data, where management strategy can mask species effects. By contrast, species effects are present in P-parameters.

Moreover, all eco-physiological parameters are driven by environment and evolutionary selection. Inter-specific variability should be statistically distinguishable from environmentally induced variability. For example here, too few data are available to screen environmental effects or to perform robust statistical tests on all parameters. Thus co-linearity between environment and trait values can potentially bias the classification. However, most PFTs in DGVMs are

367 currently parameterized without screening out possible environmental effects, and their
368 parameterization is usually based on far fewer references than the 156 data used here (Zaehle
369 *et al.*, 2005; Alton, 2011; Wullschleger *et al.*, 2014). The method used in this study is thus
370 relevant for use with DGVMs other than ORCHIDEE-FM.

371 Past studies sought to define PFTs by finding an optimal set of traits (Pillar & Sosinski, 2003;
372 Bernhardt-Römermann *et al.*, 2008; Boulangeat *et al.*, 2012). In contrast, in this study we started
373 from the modelling viewpoint and sought to define PFTs by selecting key functional traits
374 related to parameter values. We managed to define two different PFTs from TNF: one group is
375 formed by pines: *Pinus pinaster* and *Pinus sylvestris*, and the other by spruces and firs: *Abies*
376 *alba*, *Picea abies* and *Pseudotsuga menziesii*. We can see that the classification results in the
377 separation of species with *pinus* trees clustered together, arguing for a genus-based
378 classification. Liston *et al.* (1999) already demonstrated clear phylogenetic differences between
379 pines and spruces. However, all eco-physiological parameters are driven by environment and
380 strong selections have been operating for a long time on these species. Thus, the grouping of
381 pines in a same cluster may be the result of parallel acclimatization of species sharing the same
382 bio-climatic conditions.

383 This proposed re-classification of the TNF of France into two PFTs seems to explain the spatial
384 distribution of simulated misfits of the volume and volume increment in Bellassen *et al.* (2011)
385 (Fig.4, Sup.Fig.3), even within pixels where the two PFTs are present (Fig. 4b). Moreover, the
386 use of two PFTs improves the spatial correlation between observed and simulated stand
387 variables by more than 40 %, while the use of one PFT by species does not bring more precision.
388 This result tends to confirm our method and that the differences between simulated and
389 observed stands are mostly attributable to the PFT representation rather than a potential bias
390 linked to local soil-climate conditions. Past studies highlighted the discrepancies between the
391 leaf and the canopy scale, but also the structural uncertainties of current DGVMs, which

392 therefore cannot be parameterized with leaf-scale observations (Bonan *et al.*, 2012). Difficulties
393 in parameterizing one unique PFT can also arise from the heterogeneity of species within this
394 PFT.

395 **Inconsistencies between parameter values from eddy-covariance and literature data**

396 The inconsistency between the literature review and eddy-covariance (EC) based optimization
397 results from Kuppel *et al.* (2014) implies that the Bayesian optimization based on variables like
398 fluxes (which depend on many parameters) is inadequate because it does not correctly represent
399 physiological processes. The optimization method may benefit from the growing availability of
400 trait observations in the TRY database. However, as highlighted by Bonan *et al.* (2012), it also
401 suggests that some fundamental processes in ORCHIDEE-FM are lacking or poorly
402 represented, thus leading to compensations in the parameterization.

403 We have no information about the correlation of optimized parameter errors related to
404 temperate needleleaf forest in Kuppel *et al.* (2014). However, Kuppel (2012) showed strong
405 posterior error correlations between the carboxylation rate, the needle lifespan and the optimal
406 temperature for example when considering all multi-site optimizations and all PFTs (see
407 Fig.S13 of Kuppel (2012) for the correlation matrix of parameters errors). These correlations
408 occur because of the inability (or equifinality, i.e. different combinations of parameter values
409 can lead to the same result) of EC data to discriminate the value of each single parameter. Traits
410 optimized in Kuppel *et al.* (2014) can be biased due to equifinality or a poor representation of
411 some processes, thus leading to an over-parameterization when constrained by EC data.

412 In the other hand, parameters optimized by Kuppel *et al.* (2014) represent traits integrated at
413 the canopy level, while measurements gathered in this study were performed on individual
414 leaves. Therefore, the comparison between optimized and measured traits should be made in
415 the light of the different biases specific to each method and scale.

416 These differences between leaf-scale measurements of parameters from literature data and the
417 values optimized using ecosystem-level observations of fluxes of NEE, H, and E can be
418 attributed to the lack of physiological consideration in the mathematical procedure used to
419 optimize parameters from ecosystem-scale flux data. Despite the constraint imposed by setting
420 a realistic prior error value for each parameter in the inversion (based on expert judgment), the
421 minimization of a Bayesian cost function produces a posterior value based on purely
422 mathematical criteria. Such a value may work well locally, but might be disconnected from eco-
423 physiological reality (Pelikan 2005; Ward *et al.*, 2010). This discrepancy can arise from the
424 erroneous representation of eco-physiological processes in ORCHIDEE, but also
425 compensations or co-variations between parameters dealing with same eco-physiological
426 processes that cannot be separated by NEE measurements alone. Another point revealed by this
427 study is the potential bias introduced by giving equal weight to all the geographic sites used for
428 optimization. Most of the sites (20 in total) optimized in Kuppel (2012) were *Picea abies* and
429 *Pinus sylvestris* whereas the only site optimized by Santaren *et al.* (2007) was *Pinus pinaster*.
430 In the end, parameter values of optimizations were allocated to the same PFT, ignoring the
431 different species. However we show here differences between species for key parameters inside
432 the same plant functional type. The problem highlighted here is an over-representation of one
433 species in the optimization. Unless this over-representation reflects the real species distribution
434 on the ground, it will bias the final value retained for the global PFT. Especially in the Northern
435 Hemisphere, where we expect an increase in conifer plantations to meet the objectives of
436 climate change mitigation, the non-representation of the different capacity of species will lead
437 to the wrong estimation of carbon stocks and fluxes (Vallet *et al.*, 2009; Matthews *et al.*, 2014).
438 Our results thus highlight the importance of confronting the results of “brute force” parameter
439 calibration methods using mathematics and EC data with a more refined approach based on
440 eco-physiological knowledge before using them for model improvement.

The use of a literature review as performed in this study can provide better optimizations by applying appropriated ranges of variability for each parameter. One of the limitations of a literature search however, is the lack of data harmonization related to differences in environmental conditions and methodologies. We tried to correct for some methodological effects but too few data were available to allow a correction based on biotic and abiotic environmental as well as management factors, which leads to large spread in parameter estimates (Fig. 2). Results obtained for each parameter and the associated uncertainties are debated in detail in the extended discussion (Appendix S4).

CONCLUSION& PERSPECTIVES

In this study we proposed a new method combining literature review and hierarchical classification to constrain sensitive parameters in a DGVM model. The model used was ORCHIDEE FM and our results are model-specific, but the approach is applicable to any other DGVM with a discrete representation of PFTs. We proposed to group species into coherent groups based on parameter similarity for refining the number of PFTs. This method was applied to temperate conifers in France for 5 dominant species, and resulted in the successful derivation of two PFTs with coherent parameters. The parsimonious choice of two new PFTs to describe TNF improved the spatial representation of conifers stands carbon dynamics by more than 40% compared to the reference simulation where all TNF have the same parameter values. However using a more refined representation with PFT per species did not improve the simulations, and did not degrade them either. Our approach of coherent parameter classification is thus a good compromise between the too rigid simple PFT representation and a more complicated fully trait-based continuous parameterization of vegetation parameters in DGVMs. Thanks to the increasing availability of trait observation in global databases, our method could be applied to

refine other PFTs, for instance the “temperate broadleaf forests” PFT which currently groups together in a model like ORCHIDEE species with different characteristics such as fast growing pioneer species (*Populus sp.*) and slow growing dominant species like oak (*Quercus sp.*)

In addition, we showed clear discrepancies between observed parameter values and values optimized against eddy covariance flux measurement. This result highlights the importance of confronting the results of “brute force” parameter calibration methods with a more refined eco-physiological knowledge. We argue that this warrants further research for a better understanding of the definition of parameters, their characterization and the adequacy of point-based field observations to parameterize grid-based models.

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Data Accessibility

All data and sources used in this study are listed in Appendix S3.

488 **Biosketch**

489 M. Peaucelle did his PhD at the Climate and Environment Science Laboratory (LSCE, France).
490 His research focuses on improving the representation of temperate forest in the ORCHIDEE
491 DGVM. In particular, he is interested in improving the representation of plant functional types
492 by a more continuous approach exploring different ways to include the plasticity of plant
493 functional traits.

494 **Supporting information**

495 Appendix S1: Supplementary tables and figures (list below)

496 Table S1a: Optimized parameters from Kuppel (2012).

497 Table S1b: Parameters used in the sensitivity analysis from Bellassen *et al.*, (2010).

498 Table S2: Data sources for French silvicultural reference systems.

499 Figure S1: Representation of the relative difference between observed and simulated
500 stand volume and volume increment.

501 Figure S2: Representation of the Mahalanobis' distance between each species for
502 photosynthesis and biomass parameters.

503 Figure S3: Spatial distribution of the two new PFTs over France.

504 Figure S4: Evolution of the relative density index against the dominant height over a
505 rotation for a stand of *Picea abies*

506 Appendix S2: Detailed methodology for the literature review, the homogenization of values
507 for each parameter.

508 Appendix S3: List of references retrieved for each parameter.

509 Appendix S4: Extended discussion about uncertainties associated with each parameter.

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Parameter	Description	Equation used in ORCHIDEE-FM	Processes involved
V_{cmax_opt}	Optimal maximum rate of carboxylation ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	$V_c = \frac{V_{cmax_opt} \times C_i}{C_i + K_c \left(1 - \frac{O_i}{K_o}\right)}$ <p> V_c= RUBISCO activity ($\mu\text{molCO}_2 \text{ m}^{-2}\text{s}^{-1}$) O_i= intracellular oxygen concentration K_c and K_o=Michaelis-Menten constants of RUBISCO activity </p>	Impacts the gross primary production and substantially the stomatal conductance
T_{opt}	Optimal temperature of photosynthesis ($^{\circ}\text{C}$)	$V_c = V_{cmax_opt} \times \frac{(T_{air} - T_{max})(T_{air} - T_{min})}{(T_{air} - T_{max})(T_{air} - T_{min}) - (T_{air} - T_{opt})^2}$ <p> T_{air}= Air temperature ($^{\circ}\text{C}$) T_{min}, T_{max}= minimal and maximal temperature of photosynthesis ($^{\circ}\text{C}$) </p>	<p>Impacts the temperature dependency of the photosynthesis, and daily and seasonal variations of the GPP.</p> <p>It is the same equation used for V_{jmax} (maximal rate of the RuBP regeneration)</p>
g_{slope}	Slope of stomatal conductance in the Ball-Berry model (unitless)	$g_s = g_{min} + g_{slope} \times A \times \frac{hr}{C_a}$ <p> g_s= stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$) A = net assimilation of the photosynthesis ($\text{mol m}^{-2} \text{s}^{-1}$) hr = relative humidity (unitless) C_a = boundary layer CO_2 concentration ($\mu\text{mol mol}^{-1}$) g_{min} = empirical coefficients ($\text{mol m}^{-2} \text{s}^{-1}$) </p>	Parameter which modifies the slope of the linear relationship between the stomatal conductance and the assimilation. It substantially impacts the estimation of the NEE and E.
SLA	Specific length area ($\text{mm}^2 \text{mgC}^{-1}$)	$LAI = SLA \times Bm_{leaves}$ <p> LAI= Leaf area index ($\text{m}^2 \text{leaves m}^{-2}\text{ground}$) Bm_{leaves}= leaves biomass (mgC) </p>	Parameter which determines the Leaf Area Index and impacts the GPP.
$L_{age,crit}$	Critical leaf age for leaf senescence (month)	$V_c = V_{cmax_opt} \times e_{rel} \left(\frac{af}{Leaf_{agecrit}} \right)$ <p> af= leaf age $Leaf_{agecrit}$= mean leaf lifespan e_{rel}=relative efficiency </p>	<p>Parameter which determines the mean leaf lifespan.</p> <p>It impacts the photosynthetic activity and the senescence of leaves.</p>

V_{jmax}/V_{cmax}	Maximum flux of electron / maximum rate of carboxylation ratio (unitless)	$V_{jmax} = 2 \times V_{cmax}$ $V_{jmax} = \text{maximal rate of the RuBP regeneration } (\mu\text{mol m}^{-2}\text{s}^{-1})$	The parameter impacts the estimation of the GPP and substantially impacts the stomatal conductance.
a_{bc}	Coefficient of biomass-circumference allometry	$M = a_{bc} \times D^{b_{bc}}$ $M = \text{total aboveground tree dry biomass (kg)}$ $D = \text{diameter at breast height (cm)}$	Determines the circumference of trees and impacts thinning events and the exportation of biomass
b_{bc}	Coefficient of biomass-circumference allometry		
α_{st}	Coefficient of self thinning equation	$dens_{max} = \frac{\alpha_{st}}{Dg\beta_{st}}$ $dens_{max} = \text{stand maximum density in ind ha}^{-1} \text{ (individuals per hectare)}$ $Dg = \text{quadratic mean diameter (meters)}.$	Determines the maximal density of trees in the stand. Impacts thinning events and consequently the biomass distribution among trees
β_{st}	Coefficient of self thinning equation		
rdi_target	Targeted value or relative density index (unitless)	$thinningifrdi = rdi_{target} \pm \delta rdi$ $rdi = \text{relative density index}$ $\delta rdi = \text{tolerable variation of rdi around rdi_target}$	Determines the moment when the thinning occurs. Impacts the biomass and exportation

Table 1: List of parameters, equations and processes involved in ORCHIDEE-FM and selected for this study.

657

Parameter	Number of data from literature / TRY					Total
	<i>Abies alba</i>	<i>Picea abies</i>	<i>Pinus pinaster</i>	<i>Pinus sylvestris</i>	<i>Pseudotsuga menziesii</i>	
V_{cmax25}	13 / 0	30 / 3	13 / 0	15 / 2	20 / 0	93
T_{opt}	2 / 0	2 / 0	2 / 0	2 / 0	2 / 0	10
g_{slope}	0 / 0	7 / 6	2 / 0	8 / 0	0 / 0	23
g_{smax}	10 / 0	20 / 1	21 / 0	18 / 1	15 / 0	86
SLA	3 / 23	13 / 10	20 / 3	24 / 224	10 / 6	336
$L_{age,crit}$	2 / 2	7 / 2	7 / 0	17 / 4	4 / 2	47
J_{max}/V_{cmax}	19 / 0	25 / 2	7 / 0	11 / 1	5 / 0	70
b_{bc}	3 / 0	39 / 0	3 / 0	22 / 0	12 / 0	79
α_{st}	2 / 0	6 / 0	3 / 0	8 / 0	4 / 0	23
Rdi_{target}	1 / 0	1 / 0	1 / 0	1 / 0	1 / 0	5

658

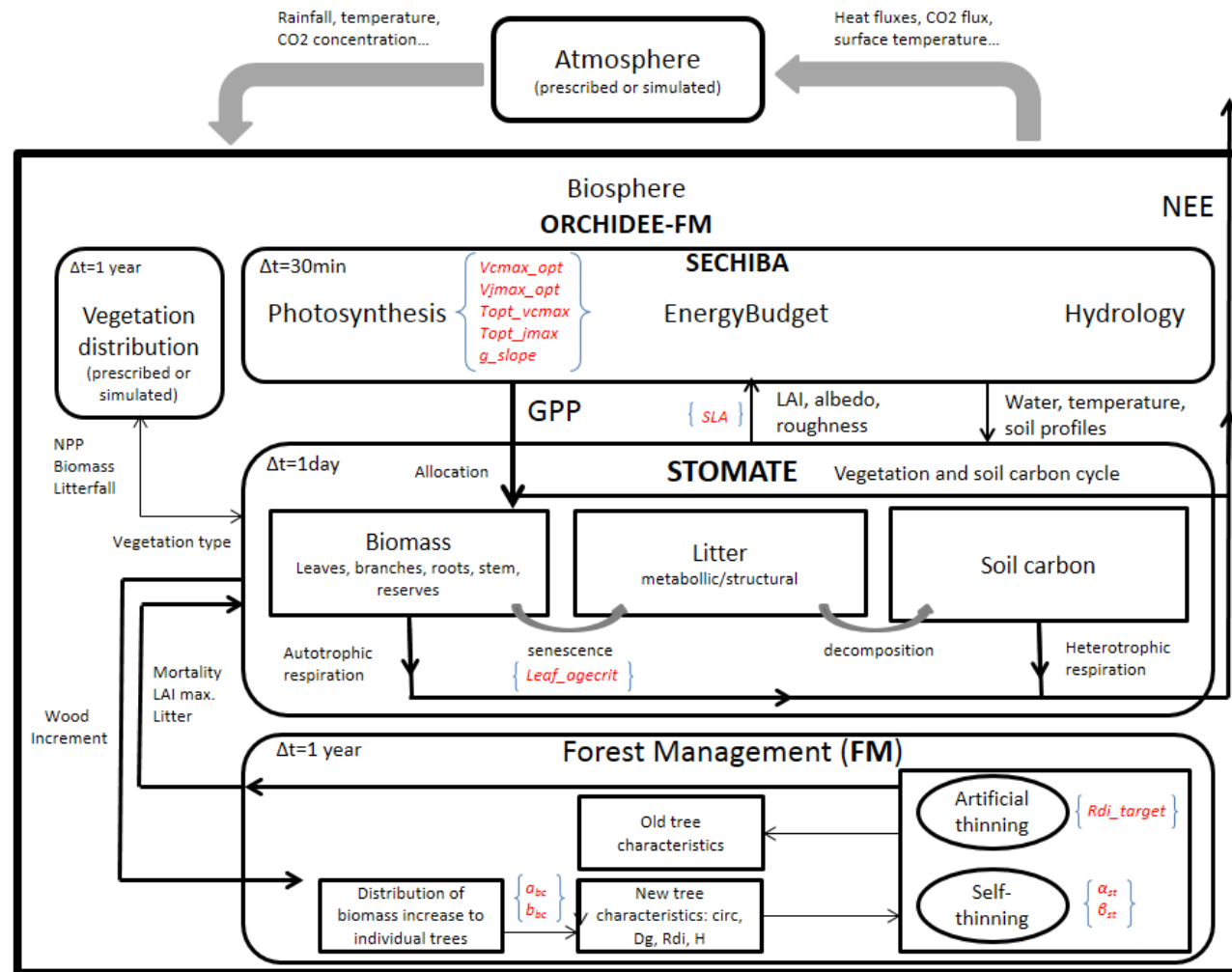
659 Table 2: Number of observations retrieved for each parameter from the literature and the TRY database. Refers to Table 1 for the description of
660 each parameter.

661

662

Parameter	Description	Current value	Santaren <i>et al.</i> , 2007	Kuppel <i>et al.</i> , 2014	Median value from literature								Unit
		TNF	TNF	TNF	<i>A.alb</i>	<i>P.abi</i>	<i>P.men</i>	<i>P.syl</i>	<i>P.pin</i>	PFT1	PFT2	TNF	
V_{cmax25}	Optimal maximum rate of carboxylation	35	41.7	31.94	46	46.77	38.35	106.61	90.3	45.5	100.2	61	μmol m ⁻² s ⁻¹
T_{opt}	Optimal temperature of photosynthesis	25	-	17.49	36.81	31.58	29.94	27.56	38.84	31.78	33.2	32.34	Vmax °C
		25	-	17.49	33.20	21.76	27.3	19.89	36.87	27.42	28.38	27.8	Jmax °C
g_{slope}	Slope of stomatal conductance in the Ball-Berry model	9	8.1	8.841	-	5.94	-	5.59	10.05	-	-	-	unitless
gS_{max}	Maximal stomatal conductance	-	-	-	3.41	3.88	4.12	3.9	3	3.89	3.78	3.89	mm s ⁻¹
SLA	Specific length area	4.63	-	10	5.51	5.4	7.08	4.73	3.1	5.6	4.73	4.85	mm ² mg ⁻¹
$L_{age,crit}$	Critical leaf age for leaf senescence	29.5	-	35.6	98.7	102.33	65.4	34	51	78	42.5	51	Months
J_{max}/V_{cmax}	Maximum flux of electron / maximum rate of carboxylation ratio	2	-	-	2.2	2.2	3.01	2.1	2.5	2.2	2.1	2.2	unitless
a_{bc}	Coefficient of biomass-circumference allometry	7.03b _{bc} ^{-4.76}	-	-	-	-	-	-	-	-	-	-	kgDM
b_{bc}	Coefficient of biomass-circumference allometry	2.295	-	-	2.52	2.36	2.4035	2.2355	2.13	2.37	2.234	2.355	ln(kgDM) ln(m) ⁻¹
α_{st}	Coefficient of self thinning equation	12,2	-	-	12.548	12.7925	12.3165	12.48097	12.544	12.4995	12.544	12.5	ln(ind ha ⁻¹)
β_{st}	Coefficient of self thinning equation	1.6	-	-	1.7505	1.664	1.6255	1.7915	1.815	1.664	1.815	1.7295	ln(ind ha ⁻¹) ln(m) ⁻¹
Rdi_{target}	Targeted value or relative density index	0.75	-	-	0.59	0.54	0.63	0.44	0.59	0.56	0.64	0.56	unitless

Table 3: Default (ORCHIDEE current value), optimized (Santaren *et al.*, 2007; Kuppel *et al.*, 2014) and observed (from the literature and the TRY database) values for each parameter used in this study. TNF correspond to the current Temperate Needleleaf evergreen Forest plant functional type. (-): no data available.



667

668 Fig.1: Representation of the ORCHIDEE-FM model and related processes. Round corner boxes correspond to ORCHIDEE modules (bold). The
 669 main simulated processes and the corresponding time step (Δt) are listed for each module. In the STOMATE module are listed the different
 670 carbon compartments, while the FM module illustrates the management processes simulated by ORCHIDEE. Arrows represent shared variables,
 671 processes and the different links between modules. Parameters used in this study are listed in parenthesis (Table 1).

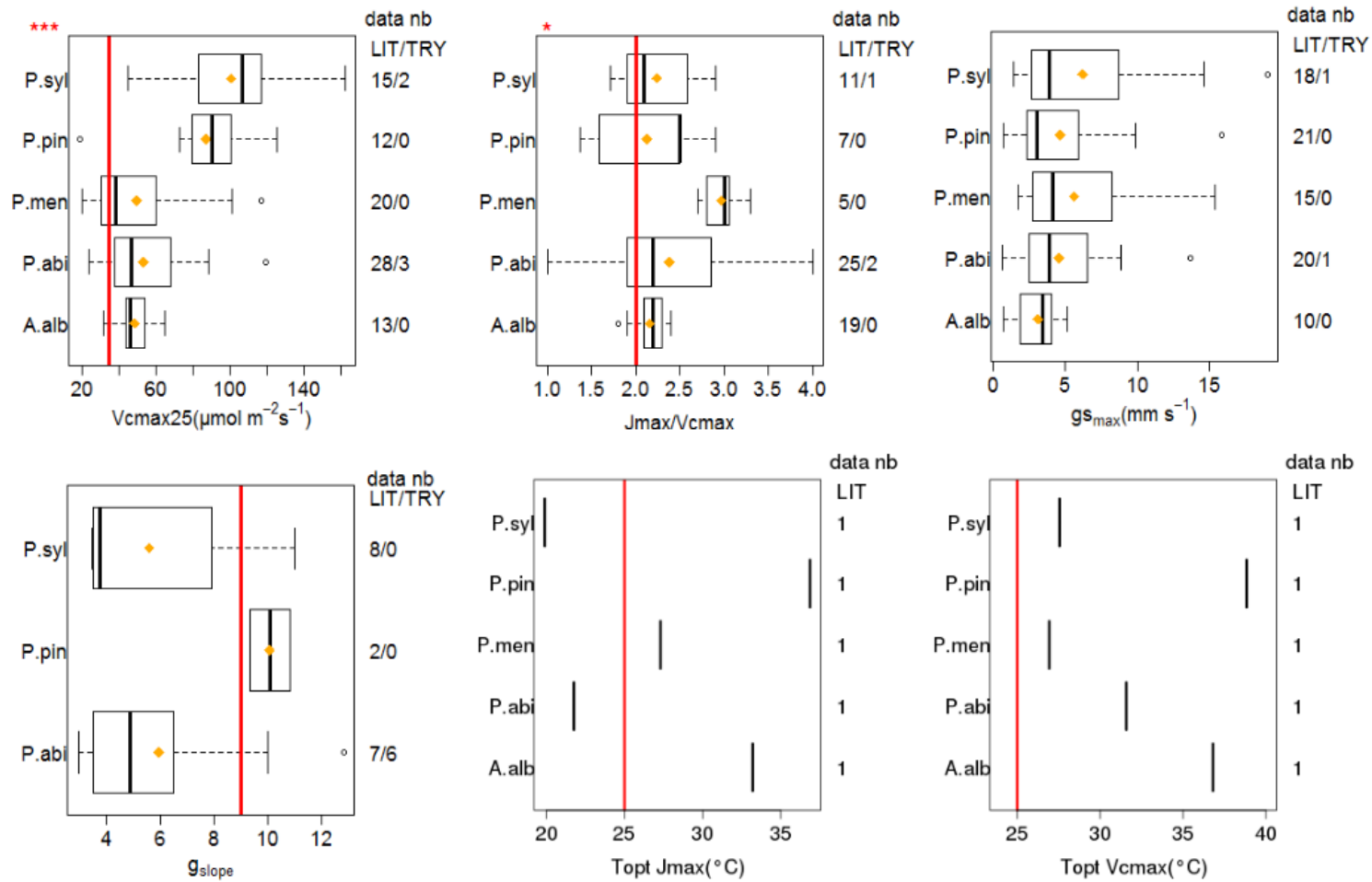


Fig.2:Boxplot representation of parameters for each species (median, first and third quartile, first and last deciles, black open circles represent values outside 1.5 times the interquartile range above the upper quartile and below the lower quartile). Refers to Table 1 for the description of each parameter. Orange diamond represent mean values; blue dots represent values fitted on French national forest inventories data. Number of data available for each species is specified on the right of each boxplot. LIT/TRY correspond to the number of data from literature and from the

677 TRY database. The red line represents the current ORCHIDEE value of the TNF PFT. Parameters with significant Kruskal-Wallis test : '*' p-
678 value < 0.05; '***' p-value < 0.01

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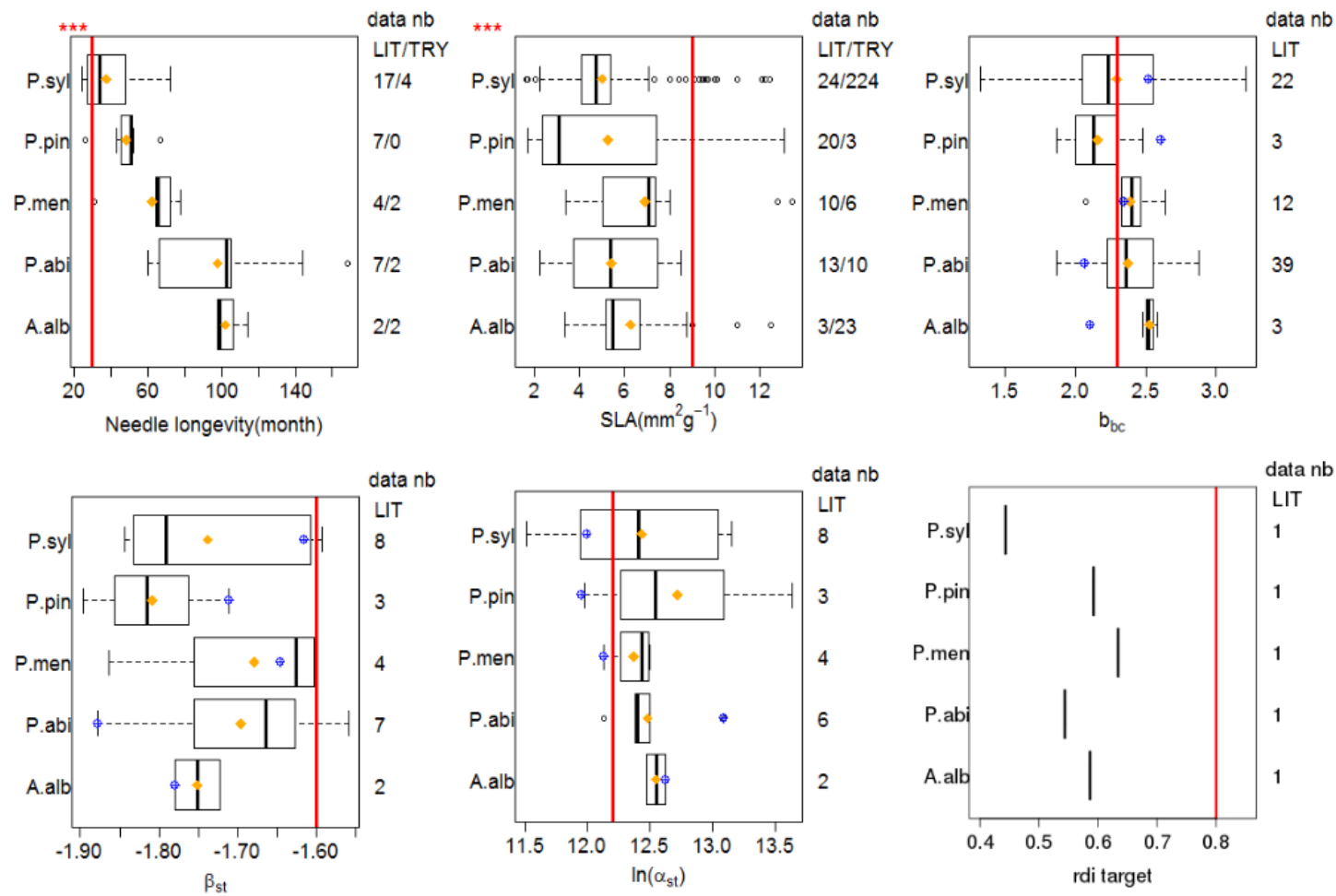
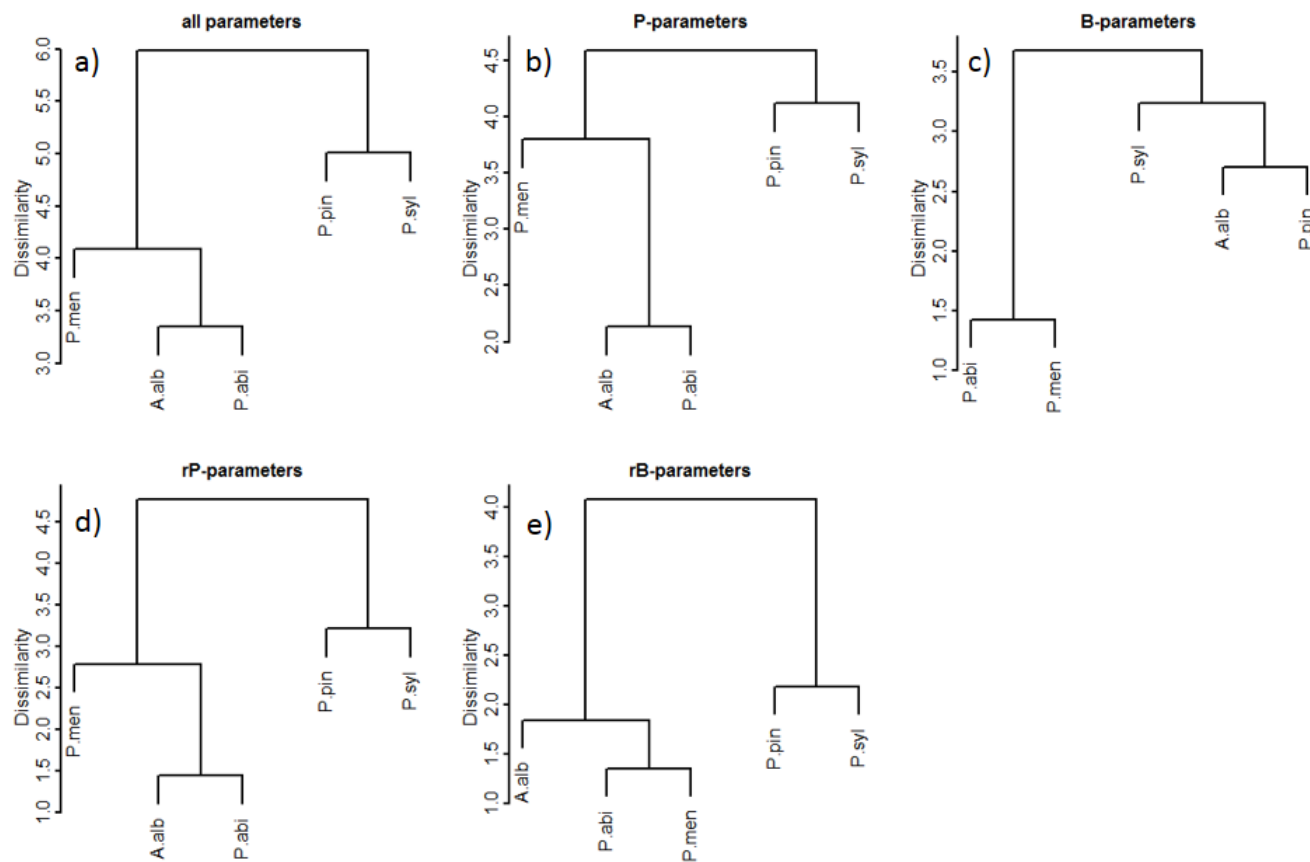
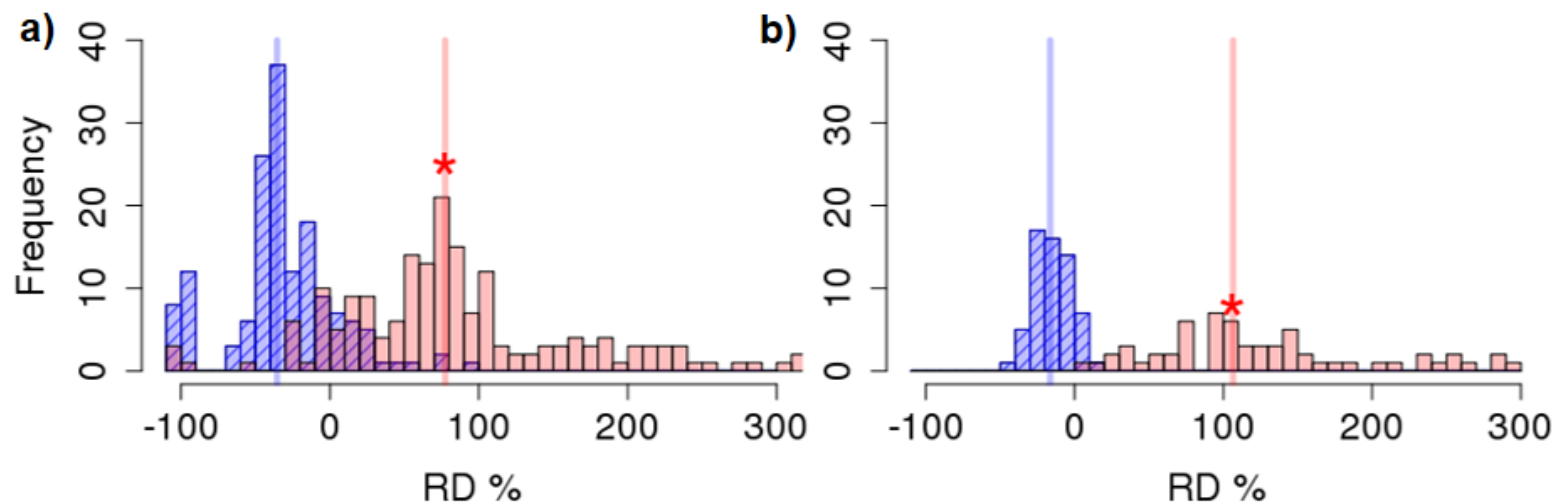


Fig.2 (contd.)



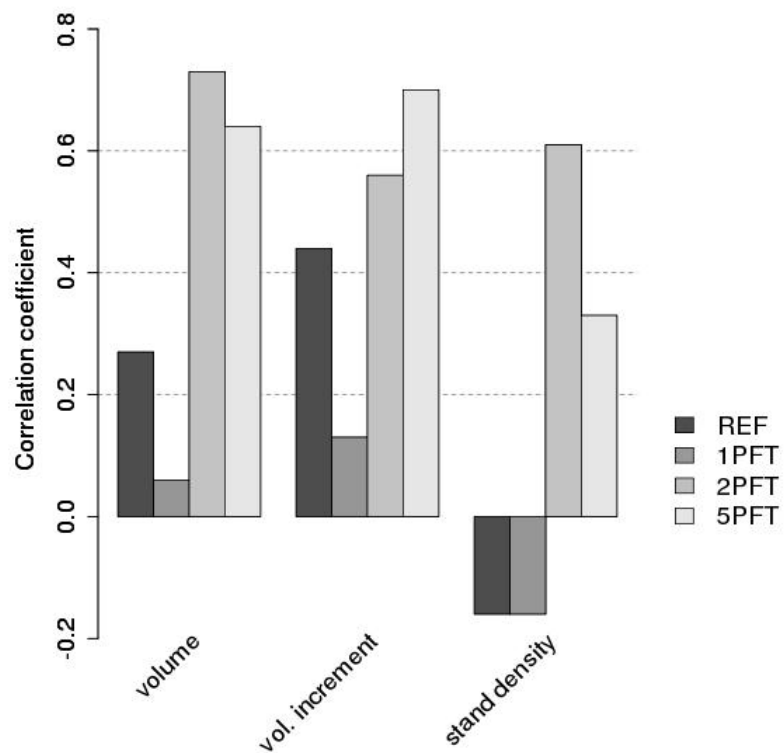
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684 Fig.3: Clusters of species (*Abies alba*/ *Picea abies*/ *Pseudotsuga mensieziei*/ *Pinus sylvestris*/ *Pinus pinaster*) obtained with different parameter
685 selections. a) with all parameters; b) with photosynthesis-parameters (P); c) with biomass and management-parameters (B); d) with a reduced set
686 of P-parameters (rP) and e) with a reduced set of B-parameters (rB) and f) with significantly different parameters between species.



687
 688 Fig.4: Distribution of the mean relative difference (“RD %”) between observed and simulated volume increment in Bellassen *et al.*, (2011)
 689 according to the new PFT classification for a) pixels where only one PFT is present and b) where both PFTs are present on the same pixel. Blue
 690 striped frequencies represent PFT1 (*Abies alba/ Picea abies/ Pseudotsuga mensiezii*), red frequencies PFT2 (*Pinus sylvestris/ Pinus pinaster*).
 691 Vertical lines represent the median relative difference for each PFT. The asterisk indicates a significant difference between the two means at
 692 $P < 0.05$

693



694

695 Fig.5: Spearman's correlation coefficient between observed and simulated volume, volume
 696 increment and stand density for simulations: REF (standard), S1 (1 PFT), S2 (2 PFTs) and S3
 697 (5 PFTs). Results are for 50y old stands over France