

*The impact of alternative trait-scaling hypotheses for the maximum photosynthetic carboxylation rate ( $V_{cmax}$ ) on global gross primary production*

Article

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1 **The impact of alternative  $V_{\text{cmax}}$  trait-scaling hypotheses on global gross primary**  
2 **production**

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47

48 **Summary**

- 49 • The maximum carboxylation rate of photosynthesis ( $V_{\text{cmax}}$ ) is an influential plant trait  
50 that has multiple scaling hypotheses, which is a source of uncertainty in predictive  
51 understanding of global gross primary production (GPP).
- 52 • Four trait-scaling hypotheses (plant functional type, nutrient limitation, environmental  
53 filtering, and plant plasticity) with nine specific implementations are used to predict  
54 global  $V_{\text{cmax}}$  distributions and their impact on global GPP in the Sheffield Dynamic  
55 Global Vegetation Model.
- 56 • Global GPP varied from 108.1 to 128.2 PgC  $y^{-1}$ , 65 % the range of a recent model  
57 intercomparison of global GPP. The variation in GPP propagated through to a 27%  
58 coefficient of variation in net biome productivity (NBP). All hypotheses produced  
59 global GPP highly correlated ( $r=0.85-0.91$ ) with three proxies of global GPP.
- 60 • Plant functional type based nutrient limitation, underpinned by a core SDGVM  
61 hypothesis that plant nitrogen status is inversely related to increasing costs of N  
62 acquisition with increasing soil C, adequately reproduced global GPP distributions.  
63 Further improvement could be achieved with accurate representation of water  
64 sensitivity and agriculture in SDGVM. Mismatch between environmental filtering  
65 (the most data-driven hypothesis) and GPP suggested that greater effort is needed  
66 understand  $V_{\text{cmax}}$  variation in the field, particularly in northern latitudes.

67

68

69 **Key Words:**

70 Gross Primary Production, Modelling photosynthesis, Plant functional traits, Trait-  
71 based modelling, Terrestrial carbon cycle, Co-ordination hypothesis, DGVM, Assumption  
72 centred modelling

73

## 74 **Introduction**

75           Photosynthetic carbon assimilation is the largest flux in the global carbon cycle, and  
76 accurate future projections from terrestrial biosphere models (TBMs) rely upon accurate  
77 representations of photosynthesis. Rates of photosynthesis are most commonly simulated as  
78 the minimum carboxylation rate of two processes—the Calvin-Benson cycle and light  
79 activated electron transport—modelled using Michaelis-Menten principles of enzyme kinetics  
80 (Farquhar & Wong, 1984; Collatz *et al.*, 1991; Harley *et al.*, 1992; von Caemmerer, 2000).  
81 These two realised rates are sensitive to their respective maximum rates—the maximum  
82 carboxylation rate ( $V_{\text{cmax}}$ ) and the maximum electron transport rate ( $J_{\text{max}}$ ), and terrestrial  
83 carbon cycle models are highly sensitive to these parameters (Zaehle *et al.*, 2005; Bonan *et*  
84 *al.*, 2011; Sargsyan *et al.*, 2014; Rogers, 2014; Rogers *et al.*, 2017). Many methods are used  
85 across TBMs to calculate  $V_{\text{cmax}}$  and  $J_{\text{max}}$ , and these methods represent competing hypotheses,  
86 formally or informally posed, on how these influential plant traits scale geographically. The  
87 diversity of hypotheses potentially leads to large, and previously unquantified, variation in  
88 the simulation of global photosynthetic carbon assimilation and poses the broader scientific  
89 question: what are the primary drivers of global  $V_{\text{cmax}}$  scaling?

90           Plant functional traits consist of a wide range of measurable plant phenotypic  
91 (chemical, physiological, and structural) properties that convey information pertaining to  
92 some aspect of plant function, and thus are used to describe plant function and functional  
93 diversity. Correlations between functional traits have been used to define common axes of  
94 plant strategies (Grime, 1974; Craine *et al.*, 2002; Wright *et al.*, 2004; Reich, 2014) and  
95 discrete plant functional types (PFTs), designed to simplify the diversity of plant life within a  
96 tractable modelling framework (Woodward & Cramer, 1996; Smith *et al.*, 1998; Wullschleger  
97 *et al.*, 2014). The quantitative nature of plant functional traits lends their use to global  
98 simulation modelling, allowing functions that represent the multiple ecosystem processes  
99 encoded in TBMs to be parameterised using values of the relevant plant functional traits.  
100 Recently, much attention has been paid to acknowledging wider and continuous variation in  
101 plant functional traits within ecosystem modelling (van Bodegom *et al.*, 2012, 2014; Scheiter  
102 *et al.*, 2013; Pavlick *et al.*, 2013; Verheijen *et al.*, 2013; Fyllas *et al.*, 2014; Fisher *et al.*,  
103 2015; Kueppers *et al.*, 2016). Modelling this trait variation requires spatial and temporal trait-

104 scaling hypotheses that go beyond the implicit hypothesis for many traits in many TBMs—  
105 that traits scale discretely across, and are static within, a limited set of broadly defined PFTs.

106 In the current study, multiple competing trait-scaling hypotheses for  $V_{\text{cmax}}$  and their  
107 impacts on global patterns of gross primary production (GPP) are assessed within a common  
108 modelling framework (the Sheffield Dynamic Global Vegetation Model—SDGVM). Broadly  
109 defined, four  $V_{\text{cmax}}$  scaling hypotheses are investigated: 1) discrete PFT variation, 2) nutrient  
110 limitation, 3) environmental filtering, and 4) plant plasticity allowing acclimation to  
111 environment. As described above, discrete PFT variation, is an hypothesis designed to  
112 represent key features of global diversity in plant function within a tractable modelling  
113 framework.

114 In more detail, nutrient, specifically nitrogen (N), limitation is hypothesised to affect  
115  $V_{\text{cmax},25}$  due to the high concentrations of the enzyme RuBisCO in leaves which makes up a  
116 large portion of whole plant N demand. Empirically,  $V_{\text{cmax},25}$  and photosynthetic rates correlate  
117 with leaf N (Field & Mooney, 1986; Wright *et al.*, 2004; Kattge *et al.*, 2009) and plant N  
118 uptake (Woodward & Smith, 1995). SDGVM incorporates the hypothesis that plant N status  
119 is based on the principle of costs associated with plant N uptake as soil C increases and  
120 across mycorrhizal types (Read, 1991; Woodward *et al.*, 1995). This hypothesis has been  
121 expanded on by recent model development efforts (Fisher *et al.*, 2010; Brzostek *et al.*, 2014).  
122 The environmental filtering hypothesis states that adaptation to local environment is the  
123 primary determinant of  $V_{\text{cmax},25}$  scaling. In our study, a data driven approach was taken to  
124 represent environmental filtering of  $V_{\text{cmax},25}$  following Verheijen *et al.*, (2013). Plant plasticity,  
125 which allows acclimation to environment, is based on the hypothesis that the process of  
126 natural selection has created plants able to respond to their environment at shorter timescales  
127 (e.g. days to weeks). These plant centric methods tend to consider an optimality perspective  
128 whereby plants adjust  $V_{\text{cmax}}$  to maximise the difference between costs and benefits (Chen *et al.*,  
129 1993; Maire *et al.*, 2012; Prentice *et al.*, 2014).

130 Our aims were to quantify and understand the causes of variability across these  
131 various scaling hypotheses of: 1) global  $V_{\text{cmax}}$  distributions; 2) simulated global distributions  
132 of GPP; and 3) temporal trends in global GPP and subsequent impacts on net biome  
133 productivity, the simulations of which is the primary purpose of global TBMs. To evaluate the  
134 spatial patterns of global GPP predicted by the various methods to scale  $V_{\text{cmax}}$  we use a

135 number of global GPP observation proxies: the Max Plank Institute (MPI) upscaled eddy-flux  
136 estimate of GPP (Jung et al., 2011); global solar induced fluorescence (SIF) from the GOME-  
137 2 instrument (Joiner et al., 2013, 2016), and the CASA model calibrated using SIF data.



138 **Methods**

139 The SDGVM was developed as a daily timestep, global biogeography and eco-  
140 physiology model (Woodward *et al.*, 1995; Woodward & Lomas, 2004) to predict the primary  
141 biomes of Earth and their associated fluxes of carbon (C) and water in response to global  
142 change. SDGVM has been described and extensively evaluated at site and global scales  
143 (Woodward *et al.*, 1995; Cramer *et al.*, 2001; Woodward & Lomas, 2004; Picard *et al.*, 2005;  
144 Sitch *et al.*, 2008; Beer *et al.*, 2010; De Kauwe *et al.*, 2013, 2014; Friend *et al.*, 2014; Walker  
145 *et al.*, 2014b; Zaehle *et al.*, 2014), so here we provide a brief description of the model and the  
146 process simulation methods relevant to this paper.

147 In SDGVM, C and water cycles conserve mass, while canopy nitrogen (N) is  
148 simulated through an empirical relationship of N uptake to soil C (Woodward *et al.*, 1995;  
149 Woodward & Lomas, 2004), based on the principle of costs associated with plant N uptake as  
150 soil C increases and across mycorrhizal types (Read, 1991). During the application of  
151 SDGVM to the FACE model data synthesis (FACE-MDS; Walker *et al.*, 2014b; Medlyn *et*  
152 *al.*, 2015) it was observed that SDGVM had low  $V_{\text{cmax},25}$  values ( $V_{\text{cmax},25} = 11N_a$ ; where  $N_a$  is  
153 leaf N per unit leaf area) and that using realistic values of  $V_{\text{cmax},25}$  observed at the FACE sites  
154 led to over prediction of GPP. The default  $V_{\text{cmax},25}$  values in SDGVM were calibrated to  
155 compensate biases caused by the assumption that photosynthesis calculated at mean daily  
156 radiation can be scaled by daylength to calculate mean daily photosynthesis. This assumption  
157 over-estimates photosynthetic efficiency by effectively linearising the response of  
158 photosynthesis to light. We corrected this bias by developing a sub-daily downscaling of light  
159 and photosynthesis calculations to 10 time periods during a half-day (described in more detail  
160 in Notes S1). The sub-daily calculation of photosynthesis allowed realistic  $V_{\text{cmax},25}$  values to  
161 generate realistic values of GPP in the model. SDGVM scales  $V_{\text{cmax},25}$  and  $J_{\text{max},25}$  by water  
162 limitation and leaf age.

163 Due to their strong correlation, in this study we focus only on  $V_{\text{cmax}}$  scaling hypotheses  
164 and employ a single relationship of  $V_{\text{cmax},25}$  to  $J_{\text{max},25}$  (Walker *et al.*, 2014a):

165 
$$J_{\text{max},25} = eV_{\text{cmax},25}^{0.890} \quad (1)$$

166 Each  $V_{\text{cmax}}$  scaling hypothesis—PFT, nutrient limitation, environmental filtering, and  
167 plant plasticity—for  $V_{\text{cmax}}$  scaling described in the introduction was implemented in the

168 SDGVM in multiple ways drawn from a number of datasets, empirical relationships, and  
169 specific mathematical representations (see below and Table 1).

170 *Static traits* (static\_PFT): Static values of  $V_{cmax,25}$  were derived by taking PFT means  
171 (using SDGVM PFT definitions; see SI for specific values) from the TRY database (www.try-  
172 db.org; data accession on 16 Nov 2010) augmented to include data from the sparsely  
173 represented tropics (described below). This augmented TRY database was also used to derive  
174 the trait-environment relationships and is described in detail below. Each trait observation  
175 was linked to a PFT based on information on growth form (shrub, grass, tree), leaf habit  
176 (deciduous/evergreen) and photosynthetic pathway ( $C_3/C_4$ ) (Verheijen et al., 2013, 2015).

177 *Nutrient limitation hypotheses*: We employ five implemetations of the nutrient  
178 limitation hypothesis. First (Ntemp\_global), the original version of SDGVM calculated  $V_{cmax}$   
179 from the rate of N uptake ( $N_u$ ) (Woodward & Smith, 1994, 1995).  $N_u$  was calculated as a  
180 function of soil C, N, and mean annual air temperature (for details see: Woodward *et al.*,  
181 1995). We label the original SDGVM method according to the assumption that sets it apart  
182 from other nutrient limitation hypotheses, that  $N_u$  is a function of temperature.

183 In later versions of SDGVM, the temperature modifier of  $N_u$  was removed and canopy  
184 N was calculated using a globally uniform, empirical scalar on  $N_u$  (Woodward *et al.*, 1995;  
185 Woodward & Lomas, 2004). All of the remaining implementations of the nutrient limitation  
186 hypotheses use the temperature independent function of  $N_u$  and canopy N. The second  
187 nutrient limitation implementation (N\_global) was:

$$188 \quad V_{cmax,25} = e^{3.712} N_a^{0.650}, \quad (2)$$

189 where  $N_a$  is leaf N, was taken from Walker *et al.*, (2014a) and was implemented globally.  
190 Third (N\_PFT), we used the PFT-specific, linear  $V_{cmax,25}$  to  $N_a$  relationships derived by Kattge  
191 *et al.*, (2009). Forth (N\_oxisolPFT), to simulate an implicit P limitation, we used the N\_PFT  
192 relationships but replaced the evergreen broadleaved PFT relationship with a relationship  
193 derived on P poor oxisols. Fifth (NP\_global), to simulate a more explicit P limitation on  
194  $V_{cmax,25}$  a function of  $V_{cmax,25}$  where P was influential in interaction with N derived from a  
195 database of field and lab grown plants (Walker *et al.*, 2014a), was also simulated:

$$196 \quad V_{cmax,25} = e^{3.946} N_a^{[0.921 + 0.282 \ln(P_a)]} P_a^{0.121}. \quad (3)$$

197 To simulate leaf P concentration we used a global relationship to total soil P derived  
198 by Ordonez et al., (2009), and a global total soil P map (Yang et al., 2014).

199 *Environmental filtering:* Environmental filtering was represented by empirically  
200 deriving PFT specific trait-environment relationships (Environ\_PFT) from the TRY database  
201  $V_{\text{cmax},25}$  values at the accession date (Niinemets, 1999; Kattge et al., 2009) augmented by  
202 Verheijen et al., (2015) to include  $V_{\text{cmax},25}$  from the tropics (Deng et al., 2004; Meir et al.,  
203 2007; Domingues et al., 2010; van de Weg et al., 2011; Cernusak et al., 2011; Azevedo &  
204 Marengo, 2012; Nascimento & Marengo, 2013) that were not well covered in the TRY  
205 database. Each species within the database was assigned to a PFT based on the specific  
206 SDGVM PFT definitions.

207 Based on the global coordinates of the trait data, each trait entry was associated to a  
208 set of environmental conditions—mean annual temperature, mean temperature of the  
209 warmest month, mean temperature of the warmest month, temperature difference of warmest  
210 month and coldest month, total annual precipitation, total precipitation in the driest quarter,  
211 fraction of total precipitation that falls in the driest quarter, mean annual relative humidity,  
212 total annual down-welling shortwave radiation—taken from the CRU-NCEP dataset (the  
213 same as used to run the model simulations). For each PFT, a multiple regression with forward  
214 selection was run to relate variation in  $V_{\text{cmax},25}$  to environmental drivers. To avoid correlation  
215 between explanatory variables, variables with a correlation over 0.7 were not used in the  
216 same regression model.

217 An empirical, linear decrease in  $V_{\text{cmax},25}$  with  $\text{CO}_2$  using the formulation of Verheijen  
218 et al., (2015) was also included as part of the response to environment (see Notes S1 for the  
219 relationships).  $V_{\text{cmax},25}$  is calculated at the beginning of each year for each PFT on each  
220 gridsquare based on mean environmental conditions of the past year.

221  $V_{\text{cmax}}$  data for C4 plants were only available for these trait-environment relationships.  
222 Therefore in the simulations for all hypotheses these relationships (or static values for  
223 static\_PFT) were used to set  $V_{\text{cmax},25}$  and phosphoenolpyruvate carboxylase (PepC<sub>25</sub>) activity  
224 in C4 plants.

225 *Plant plasticity:* We examined plant plasticity by using the co-ordination hypothesis  
226 (Co-ord\_global), which states that plants adjust  $V_{\text{cmax}}$  such that the carboxylation limited rate  
227 of photosynthesis ( $w_c$ ) equals the electron transport limited rate of photosynthesis ( $w_j$ ) over

228 mean environmental conditions, commonly considered those of the past month (Chen et al.,  
 229 1993; Maire et al., 2012). Using the Harley et al., (1992) photosynthesis functions, the co-  
 230 ordination hypothesis to find  $V_{cmax}$  requires solving the following function (see Notes S1 for  
 231 derivation):

$$0 = V_{cmax} (4C_i + 8\Gamma_*) \left[ 1 + \left( \frac{\alpha_i \bar{Q}}{S_{t,j} e^{(V_{cmax}/S_{t,v})^{0.890}}} \right)^2 \right]^{0.5} - \alpha_i \bar{Q} (C_i + K_m) \quad (4)$$

233 where  $C_i$  is the internal  $CO_2$  partial pressure (Pa),  $\Gamma_*$  is the photorespiratory  $CO_2$   
 234 compensation point (Pa),  $\alpha_i$  is the intrinsic quantum efficiency of electron transport (mol e  
 235  $mol^{-1}$  absorbed photons),  $\bar{Q}$  is the mean absorbed light intensity of the past month ( $\mu mol m^{-2} s^{-1}$ ),  
 236  $S_{t,j}$  and  $S_{t,v}$  are the temperature scalars for  $J_{max,25}$  and  $V_{cmax,25}$  to scale to leaf-temperature  
 237 from 25°C,  $e$  is the base of the natural logarithm, and  $K_m$  is the effective Michaelis-Menten  
 238 half-saturation constant for carboxylation when accounting for oxygenation (Pa). The

239 denominator in the squared term,  $S_{t,j} e^{(V_{cmax}/S_{t,v})^{0.890}}$ , represents  $J_{max}$  at the mean  
 240 temperature of the last month calculated using Eq 1 and considering temperature scaling.

241 The leaf nitrogen utilisation for assimilation (LUNA) (Xu et al., 2012; Ali et al., 2016)  
 242 hypothesis was also evaluated (LUNA\_global). LUNA optimises leaf N investment in various  
 243 photosynthetic functions—light capture, electron transport, carboxylation—to maximise daily  
 244 net photosynthesis (assimilation – leaf respiration) given mean environmental conditions (Ali  
 245 et al., 2016). The LUNA optimisation also satisfies empirical environmental constraints and  
 246 the constraint of co-ordination of  $w_c$  and  $w_j$ . Thus LUNA is a combination of plant plasticity,  
 247 nutrient limitation, and environmental filtering hypotheses.

248 In this study we use the mean environmental conditions of the past 30 days, consistent  
 249 with the averaging used for the co-ordination hypothesis (Ali et al., 2016 use the previous 10  
 250 days).

251 *Scaling of  $V_{cmax,25}$  to leaf temperature:* Being enzymatically controlled, at short  
 252 timescales  $V_{cmax}$  is highly dependent on leaf temperature and is usually normalised to a  
 253 reference temperature, commonly 25 °C, adding the subscript 25 to the notation ( $V_{cmax,25}$ ).  
 254 Three methods used to scale  $V_{cmax,25}$  to leaf temperature were investigated (Figure S1 and  
 255 Notes S1 for more details): 1) a saturating exponential (the SDGVM model default, see

256 below); 2) the Arrhenius equation modified for enzymatic loss of function at high  
257 temperatures as presented in Medlyn *et al.*, (2002); and 3) the modified Arrhenius with  
258 empirical acclimation of temperature optima to local environmental conditions (Kattge &  
259 Knorr, 2007).

260

### 261 *Model Setup & Simulations*

262 The model simulations were run using the CRU-NCEP meteorological dataset 1901-  
263 2012 (Le Quéré *et al.*, 2014; Figures S2-S4). PFT distributions were assumed static  
264 throughout the whole simulation period and were derived from land cover (LC) maps  
265 provided by the ESA CCI project ([www.esa-landcover-cci.org](http://www.esa-landcover-cci.org); Figures S5-S12). The PFT  
266 fractions were derived from the LC maps using the LC to PFT conversion described in  
267 Poulter *et al.*, (2015), and adjusted to account for the separation of C3 and C4 species that  
268 cannot be detected using MERIS wavebands (Poulter *et al.*, 2015). The resultant PFT maps  
269 were then further categorised according to the SDGVM PFT classification.

270 Atmospheric CO<sub>2</sub> data were taken from the Scripps Ocean Institute merged ice-core  
271 and flask measurement global dataset (Keeling *et al.*, 2005). The simulations were initialised  
272 with a 500 year spin-up that randomly selected meteorological years from the period 1901-  
273 1920. A separate spin-up was conducted for each ensemble member. The ensemble consisted  
274 of the nine different trait based approaches to simulate  $V_{\text{cmax}}$  (Table 1) and a subset of these  
275 nine approaches—N\_global, Co-ord\_global, and LUNA\_global—each run with the three  
276 temperature scaling assumptions, for a total of 17 simulations. N\_global, N\_PFT, Co-  
277 ord\_global, and LUNA\_global were chosen to combine with the three temperature scaling  
278 approaches to represent a range of methods, and to see how the temperature scaling  
279 assumptions interacted with the dynamic spatial-scaling plant plasticity hypotheses (i.e. Co-  
280 ord\_global, and LUNA\_global).

281

### 282 *Evaluation datasets*

283 The simulated spatial distributions of global GPP were used to evaluate the impacts of  
284 the various  $V_{\text{cmax}}$  simulation methods. No method exists to measure GPP directly at the global  
285 scale, all methods involve assumptions and models (Anav *et al.*, 2015) that may introduce

286 bias or non-independence from the SDGVM simulations. We therefore compared modelled  
 287 spatial distributions of GPP to three global GPP proxies—the empirically up-scaled flux  
 288 tower estimates of GPP from the Max Plank Institute (MPI; Beer *et al.*, 2010; Jung *et al.*,  
 289 2011); and two datasets based on GOME-2 solar induced fluorescence (SIF; Joiner *et al.*,  
 290 2013, 2016).

291 The two SIF based methods differed in their scaling of SIF radiance ( $\text{Wm}^{-2}\text{sr}^{-1}\text{y}^{-1}$ ) to  
 292 GPP ( $\text{gC m}^{-2}\text{y}^{-1}$ ). The first scaling method (SIF-CASA) scaled SIF using modelled GPP from  
 293 the Carnegie Ames Stanford Approach (CASA) Global Fire Emissions Database version 3  
 294 (GFED 3) model (van der Werf *et al.*, 2010). CASA primarily determined the spatial variation  
 295 in GPP while SIF determined the temporal variation: in each gridpoint monthly SIF data were  
 296 normalised by the gridpoint mean and then multiplied by the gridpoint mean CASA-GFED  
 297 GPP (Eq 5, SIF-CASA). The second scaling method (scaled-SIF) was intended to allow SIF  
 298 to determine both temporal and spatial variation in GPP: SIF were annually integrated in each  
 299 grid-cell, normalised by the global mean SIF ( $\bar{SIF}$ ) and then multiplied by the global mean  
 300 of the SIF-CASA dataset (Eq 6).

$$301 \quad cSIF_{i,j,t} = \frac{CASA_{i,j} \cdot SIF_{i,j,t}}{\bar{SIF}_{i,j}}, \quad (5)$$

$$302 \quad s\bar{SIF}_{i,j} = \frac{c\bar{SIF} \cdot \bar{SIF}_{i,j}}{\bar{SIF}}, \quad (6)$$

303 where CASA is the CASA GPP; cSIF is the CASA scaled GPP; sSIF is the simply scaled-SIF,  
 304 and subscripts are the gridpoint latitude, i; longitude, j; and time, t.

305 At the time of writing, SIF data were available for the period 2007-2012 and so for  
 306 consistency we present analyses for all model output over the same period. A comparison of  
 307 model results for the last full decade, 2001-2010, with 2007-2012 give quantitatively similar  
 308 results. The MPI data were available only until 2011, but given the MPI data have little inter-  
 309 annual variability (Kumar *et al.*, 2016) this was expected to have little effect.

310 GPP predicted by the trait-scaling hypotheses were compared against the three GPP  
 311 proxies using standard deviation, correlation, and centered root mean square difference.  
 312 Combining these metrics in polar co-ordinates allows comparison of gridded datasets against  
 313 a reference. These plots are known as Taylor diagrams (Taylor, 2001). Datasets were also  
 314 analysed using principle component analysis (PCA) to identify common principle axes of

315 variation across the datasets. As well as hypotheses and GPP proxies, climate variables  
316 (temperature, precipitation, and short wave radiation—SWR) were included to investigate  
317 climatic influence in the spatial patterns. Datasets were mean centred and scaled by standard  
318 deviation to give z-scores before conducting the PCA. The R (R Core Development Team,  
319 2011) package 'plotrix' (Lemon, 2006) was used to plot the Taylor diagrams and the function  
320 'prcomp' from the 'stats' package to perform the PCA.

## 321 **Results**

### 322 *Global $V_{\text{cmax},25}$ distributions*

323 Global distributions of top-leaf  $V_{\text{cmax},25}$  predicted by the various trait scaling  
324 assumptions had markedly different means, variances, and latitudinal distributions (Figure 1  
325 and S13). All but one (Ntemp\_global) nutrient limitation hypothesis including LUNA\_global  
326 (which is constrained by nutrient limitation) predicted relatively low variance in global  
327  $V_{\text{cmax},25}$ ; with moderate values in the tropics, high values in the temperate zone, highest values  
328 in dry temperate regions, and lowest values in the Boreal zone before increasing in the high  
329 Arctic (Figure 1). The exception (Ntemp\_global) showed relatively high  $V_{\text{cmax},25}$  variance with  
330 the highest values in the tropics that broadly decrease with latitude. Inclusion of phosphorus  
331 (P), either implicitly (N\_oxisolPFT; Kattge et al., 2009) for the evergreen broadleaf PFT in  
332 the simulation, or explicitly (NP\_global; Walker et al., 2014a), reduced  $V_{\text{cmax},25}$  marginally in  
333 much of the tropics (compared with N\_PFT and N\_global respectively).

334 In contrast, non-nutrient based hypotheses (Static\_PFT, Environ\_PFT, and Co-  
335 ord\_global) tended to show the opposite pattern (Figure 1 and S13): more pronounced  
336 maximum  $V_{\text{cmax},25}$  values in northern cool wet areas dominated by green needle-leaf PFTs  
337 (Scandinavia and the North-American Pacific coast) and dry areas dominated by C3 grasses  
338 (the North-American west and Central Asia). The static\_PFT values and the Environ\_PFT  
339 relationships were derived from the same  $V_{\text{cmax},25}$  dataset. Therefore the observed similar  
340 latitudinal pattern was expected, as was the more spatially homogenous distribution for the  
341 static values per PFT. The co-ordination hypothesis is independent of the datasets used to  
342 produce the static\_PFT and Environ\_PFT, and produces highest  $V_{\text{cmax},25}$  values in the coldest  
343 and driest regions—north-eastern Canada and Asia, and the Himalayan plateau.

344

### 345 *Consequences for the simulated Carbon Cycle*

346 Across the nine  $V_{\text{cmax},25}$  scaling implementations, global mean annual GPP for the  
347 period 2007-2012 ranged from 108.1 to 128.2 PgC  $\text{y}^{-1}$  (Figure 2; Table 2). The ensemble  
348 mean  $\pm$ s.d. annual GPP was  $118.7 \pm 6.4$  PgC  $\text{y}^{-1}$ , giving a coefficient of variation of 5.4 %  
349 (Table 2). The variation was somewhat higher for vegetation and soil carbon stocks (12.0 %  
350 and 13.9 %). Most crucially for carbon sequestration from the atmosphere under global  
351 change was that net biome productivity (NBP) varied by 27.1 % across the hypotheses tested.



352 The highest global GPP was simulated by the Ntemp\_global implementation of  
353 nutrient limitation, closely followed by the static PFT hypothesis at 127.8 PgC y<sup>-1</sup>. The global  
354 and PFT specific relationships of  $V_{\text{cmax},25}$  to leaf nitrogen simulated global GPP of 121.7 and  
355 116.5 PgC y<sup>-1</sup>. The inclusion of P as an additional limiting factor resulted in lower global GPP  
356 by 3.7 and 5.9 PgC y<sup>-1</sup> respectively than consideration of N limitation alone. The P related  
357 drop in GPP was a result of disproportionate GPP reduction by P in generally high  
358 productivity regions, i.e. the tropics (Figure 2 and S14). Environmental filtering  
359 (Environ\_PFT) and plant placticity (Co-ord\_global) simulated similar mean GPP at 118.1 and  
360 119.2 PgC y<sup>-1</sup>. The constrained optimisation of functional leaf N allocation (LUNA  
361 hypothesis) yielded the lowest GPP at 108.1 PgC y<sup>-1</sup>.

362 For a subset of  $V_{\text{cmax},25}$  scaling hypotheses (N\_global, LUNA\_global, Co-ord\_global),  
363 the more up-to-date modified Arrhenius temperature scaling (Medlyn et al., 2002; Kattge &  
364 Knorr, 2007) were used, both with and without acclimation of temperature optima to growth  
365 temperature. Using these temperature scaling functions generally increased global GPP  
366 (Figure S15), especially for the co-ordination hypothesis (119.1-131.2 PgC y<sup>-1</sup>). The increase  
367 in GPP for was primarily due to increasing GPP in the northern temperate and Boreal zones  
368 (Figure 3).

369 The hypotheses and their implementations also influenced the temporal trend in GPP  
370 (1900-2012) in response to increasing CO<sub>2</sub> and changing climate (Figure 4a). Ntemp\_global  
371 resulted in the strongest change in GPP over the 20<sup>th</sup> century, the result of increasing  
372 temperatures stimulating N uptake. The LUNA hypothesis and the co-ordination hypothesis  
373 both predict shallower trajectories in GPP than any of the other scaling hypotheses. Scaling  
374  $V_{\text{cmax},25}$  and  $J_{\text{max},25}$  using the modified Arrhenius function with and without temperature  
375 acclimation made little difference to the relative trajectories of GPP when used in conjunction  
376 with N\_global, co-ordination, and LUNA hypotheses (Figure S16). Across the ensemble,  
377 NBP over the period 2007-2012 was strongly related to the change in global GPP over the  
378 time period 1901-2012 (Figure 4b).

379

### 380 *Evaluating spatial distributions of GPP*

381 Overlying the general, climatically driven spatial distribution of GPP, the differences  
382 in the spatial distributions of  $V_{\text{cmax},25}$  are observable in the simulated GPP distributions (Figure

383 2 and S3). To evaluate the various hypotheses, their global GPP predictions (mean annual  
384 GPP over 2007-2012) are compared in Taylor space (Figure 5 and Table S1) with several GPP  
385 proxies (MPI, scaled-SIF, SIF-CASA; Figure 2 and S17). No matter which GPP proxy was  
386 taken as reference, all hypotheses clustered closely in Taylor space with correlation  $c. r=0.9$   
387 ( $r=0.85-0.91$ ), standard deviation within  $\pm 25\%$  (with the exception of Ntemp\_global when  
388 compared against both SIF based proxies and LUNA compared against MPI), and centred  
389 RMSD between 250 and 500  $\text{gC m}^{-2}\text{y}^{-1}$ . All hypotheses were marginally less correlated to the  
390 scaled-SIF data ( $r=0.85-0.89$ ) than the other two GPP proxies.

391 The most correlated hypotheses to MPI and SIF-CASA were N\_global and N\_PFT,  
392 though the improvements in these correlations were marginal ( $r=0.91$  vs  $0.88-0.90$ ).  
393 Ntemp\_global was generally less well correlated to all three proxies with substantially higher  
394 standard deviation and which predicted the highest global GPP and strongest latitudinal  
395 gradient. The least correlated hypotheses to MPI were LUNA\_global and Environ\_PFT,  
396 though again only marginally. Environ\_PFT was also less well correlated with both SIF based  
397 proxies. N\_PFT and N\_oxisolPFT were the most correlated to scaled-SIF, marginally better  
398 than LUNA and N\_global. The variance in the correlation across the hypotheses was greater  
399 when hypotheses were compared against the scaled SIF proxy (Figure 5c).

400 Difference plots between modelled GPP and GPP proxies (Figure 6 and S18-S19)  
401 showed that the N\_oxisolPFT implementation tended to perform well against all three  
402 proxies, though there were some substantial under-predictions in tropical forests when  
403 compared against MPI (Figure S18). However, tropical GPP was consistently under-predicted  
404 by many implementations when compared against MPI, particularly in the Amazon. Static  
405 values per PFT and Ntemp\_global clearly showed the strongest mismatches with the GPP  
406 proxies. Environ\_PFT performed poorly in northern latitudes, particularly Scandinavia, and  
407 southern China, where  $V_{\text{cmax}}$  was predicted to be higher than any other implementation  
408 (Figure 1). Co-ordination and LUNA performed well, but tended to over-predict in northern  
409 latitudes when compared against N\_PFT and N\_oxisolPFT. Across all implementations, GPP  
410 was under-predicted in Europe, eastern North America, and India while GPP was over-  
411 predicted in grasslands, particularly in South America, western North America and sub-  
412 Saharan Africa.

413           When the alternative, more realistic modified Arrhenius temperature response  
414 hypotheses were implemented, mismatches with scaled-SIF were unaffected for  
415 LUNA\_global, slightly worsened in N\_global, N\_PFT, and noticeably worsened for Co-  
416 ord\_global (Figure 5d). Implemented within the LUNA model, the three different temperature  
417 scaling assumptions made little difference to global GPP, presumably because the N  
418 constraint in LUNA was strong and the optimisation allowed flexibility around temperature  
419 responses to find a similar maximum assimilation rate across temperature scaling  
420 assumptions.

421           The SIF-CASA, scaled-SIF and MPI proxies were generally more correlated to each  
422 other than to any of the  $V_{\text{cmax}}$  hypothesis implementations, but only marginally. Arguably the  
423 proxies were as dissimilar from each other as the better model hypotheses were from the  
424 proxies, making it difficult to provide a definitive conclusion about which specific  
425 implementation of the various hypotheses was closest to GPP observation proxies.

426           Principal component (PC) analysis (PCA) was used to identify the common patterns  
427 and areas of divergence across both the models and the GPP proxies, and the potential climatic  
428 drivers of the commonalities and differences. PCA demonstrated that 82 % of the spatial  
429 variance across simulated GPP, GPP proxies, and climatic variables are explained by a single  
430 PC (Figure S20). All model assumptions are closely grouped with high loadings on PC1  
431 (Figure 7a), i.e. all model predictions are positively correlated with the spatial pattern of the  
432 first PC (Figure 7c). Closely grouped to the models on PC1 are all observed GPP proxies, as  
433 well as precipitation. Short wave radiation (SWR) and temperature were less strongly  
434 correlated with PC1, though the correlation was also positive, suggesting that precipitation is  
435 the primary driver of the dominant global pattern in GPP.

436           PC2 accounted for c. 11 % of spatial variance and segregates SWR and temperature  
437 (both positively correlated to PC2) from the model implementations, GPP proxies, and  
438 precipitation (Figure 7d). The remaining PCs combined account for 7 % of the spatial  
439 variation in the data and it is these remaining PCs that demonstrate the main areas of  
440 divergence between  $V_{\text{cmax}}$  implementations and GPP proxies.

441           PC3 and PC4 account for 4 % of variation. Short wave radiation and modelled GPP  
442 were correlated with PC3 while the GPP proxies (MPI most strongly) and precipitation were  
443 anti-correlated. PC3 shows the regions where modelled GPP is stimulated by light (primarily

444 in natural grasslands; blue areas Figure 7e) or restricted by low light (red areas). By contrast,  
445 the GPP proxies appear to be stimulated by precipitation (red areas) or restricted by low  
446 precipitation (blue areas). PC4 segregates both SIF proxies from precipitation. PC4 shows  
447 high values almost exclusively in the worlds major agricultural regions—the North American  
448 cornbelt, the Northeast and South regions of Brazil and the area surrounding São Paulo,  
449 Europe and the Russian bread basket, India, particularly north India, central eastern China,  
450 and even smaller agricultural regions such as the Indus valley in Pakistan and alongside the  
451 Rift Valley in East Africa.

## 452 Discussion

453 We tested a series of plausible trait-scaling hypotheses for  $V_{\text{cmax},25}$ , many of which are  
454 implemented in terrestrial ecosystem models, and found that they led to substantial variability  
455 in SDGVM simulated global GPP. Mean annual GPP ranged across the implementations of  
456 the hypotheses from 108.1 to 128.2 PgC  $\text{y}^{-1}$  (mean  $118.7 \pm 6.4$  PgC  $\text{y}^{-1}$ ). The range in global  
457 GPP demonstrates the large sensitivity of simulated GPP to  $V_{\text{cmax},25}$  and this range  
458 encompasses 65% of that from a set of three models run in coupled and uncoupled modes  
459 (1990-2009 mean annual GPP range of 130-161 PgC  $\text{y}^{-1}$ , mean  $145.6 \pm 12.6$  PgC  $\text{y}^{-1}$ ; Anav *et al.*  
460 *et al.*, 2015). The simulations used by Anav *et al.*, (2015) were drawn from two inter-  
461 comparison projects, each with their own protocols, which is likely to inflate the range of  
462 simulated GPP compared to the simulations presented in this study which share a single  
463 protocol. Thus variation in simulated GPP caused by  $V_{\text{cmax},25}$  trait scaling hypotheses likely  
464 represents a substantial source of variation in GPP across models, which is currently  
465 unaccounted for in model intercomparisons (e.g. Anav *et al.*, 2015).

466 Dynamic trait-scaling based on nutrient limitation, in which plant nutrient status is  
467 inversely related to the cost of N acquisition, performed better than other hypotheses when  
468 compared against three GPP observation proxies. PFT specific relationships of  $V_{\text{cmax}}$  to leaf N  
469 resulted in the best performance. Static trait values per PFT were not supported by this study.  
470 The better performance of nutrient limitation implementations was most apparent when  
471 compared against the scaled-SIF GPP proxy and we argue that this is a more independent,  
472 thus more robust, comparison.

473

### 474 Evaluation of $V_{\text{cmax}}$ distributions

475 Discerning which is the most realistic trait-scaling hypotheses was non-trivial.  
476 Currently no independent, globally gridded estimates of  $V_{\text{cmax},25}$  distributions exist. Many  
477 regions in global  $V_{\text{cmax}}$  datasets are only sparsely represented and one of the most  
478 comprehensive global  $V_{\text{cmax}}$  datasets was employed to compile the  $V_{\text{cmax},25}$  relationships to  
479 environment (Environ\_PFT) for the trait filtering hypothesis (Kattge *et al.*, 2011; Verheijen *et al.*  
480 *et al.*, 2013). The Environ\_PFT prediction of the global  $V_{\text{cmax},25}$  distribution (Figure 1) is an  
481 empirical upscaling of  $V_{\text{cmax},25}$  point measurements using global climatic and land-cover  
482 information. Unlike other hypotheses tested, which additionally rely on either model process

483 representation (e.g. simulation of leaf N) or more theoretical assumptions (e.g. co-ordination),  
484 Environ\_PFT is data-driven and contingent only on the assumption that  $V_{\text{cmax},25}$  scales with  
485 environment (coefficient of determination 0.49-0.82 for C3 plants, see Notes S1; and Ali *et*  
486 *al.*, [2015]; Verheijen *et al.*, [2013]).

487         The data-driven Environ\_PFT  $V_{\text{cmax},25}$  values are higher in northern latitudes relative  
488 to the tropics, as are  $V_{\text{cmax},25}$  distributions for the co-ordination hypothesis, which is in line  
489 with current literature (A. Rogers *et al.*, unpublished). All the N based hypotheses in SDGVM  
490 (including LUNA) generally showed higher  $V_{\text{cmax},25}$  in the tropics than in the Boreal and  
491 Tundra zones (Figure 1) which is not consistent with our data-driven estimate  
492 (Environ\_PFT). N limitation hypotheses predictions of tropical  $V_{\text{cmax},25}$  were consistent with  
493 the literature, often reported in the range 20-80  $\mu\text{molm}^{-2}\text{s}^{-1}$  (Domingues *et al.*, 2010, 2015;  
494 Vårhammar *et al.*, 2015; Norby *et al.*, 2016), but were not consistent with values reported for  
495 the high Arctic, in the range 60-160  $\mu\text{molm}^{-2}\text{s}^{-1}$  (A. Rogers *et al.*, unpublished).

496         The primary cause of the zonal  $V_{\text{cmax},25}$  distribution for the implementations  
497 constrained by N is the core SDGVM hypothesis that plant nutrient status is inversely related  
498 to soil carbon. This hypothesis is based on observations that plant N uptake decreases as  
499 dependence on organic N supply (correlated with mycorrhizal N supply) increases, which in  
500 turn is hypothesised a consequence of increasing soil organic matter (Read, 1991; Woodward  
501 *et al.*, 1995). The global distributions of  $V_{\text{cmax},25}$  predicted by the nutrient limitation hypothesis  
502 are therefore generally the inverse of the distributions of soil carbon (Figure S21-S23),  
503 resulting in a broad latitudinal gradient in leaf N as soil decomposition rates slow with  
504 cooling temperatures. This cost-based hypothesis for plant N status reproduces the broad  
505 macro-ecological pattern of increasing N limitation as latitude increases suggested by leaf  
506 C:N and N:P stoichiometry (Reich & Oleksyn, 2004; McGroddy *et al.*, 2004; Ordonez *et al.*,  
507 2009).

508         The original LUNA study at the global scale showed lower  $V_{\text{cmax},25}$  in the tropics and  
509 global distributions of top-leaf  $V_{\text{cmax},25}$  that were more similar to those predicted by  
510 Environ\_PFT and Co-ord\_global (Ali *et al.*, 2016) than the N limitation hypotheses to which  
511 LUNA was more similar in this study. The defining difference is that Ali *et al.*, (2016)  
512 assumed a constant top-leaf N of 2  $\text{gm}^{-2}$ , while in SDGVM leaf N varies as a function of soil

513 carbon. The results in SDGVM suggest that LUNA is more sensitive to variability in leaf N  
514 than to variability in environment.

515

#### 516 *Evaluation of GPP distributions*

517 Principal components analysis (PCA) demonstrated that precipitation was the primary  
518 driver of the dominant mode of global GPP distributions in both the GPP proxies and all  
519 model simulations, and was therefore responsible for the strong correlation (0.85-0.91) of all  
520 hypotheses to the proxies. PCA indicated that the model simulations diverged from the  
521 observation proxies for two reasons: 1) a relative GPP stimulation by PAR in dry grasslands  
522 in SDGVM opposing a relative GPP reduction by low precipitation in the proxies (and *vice*  
523 *versa*; PC3); and 2) a relative stimulation of GPP in SIF based proxies in agricultural areas of  
524 the planet that was anti-correlated with precipitation and that was not apparent in the  
525 SDGVM nor MPI (PC4).

526 The stimulation of GPP by PAR without a counteracting reduction from low  
527 precipitation in SDGVM is most likely due to the relative insensitivity of SDGVM to low soil  
528 water availability when compared against other models (Medlyn *et al.*, 2016). On the other  
529 hand, the ubiquity of the under-prediction in all of Earth's major agricultural regions is likely  
530 due to agricultural improvement that was not represented by SDGVM—e.g. improved seed,  
531 fertilisation, and irrigation. The negative correlation of precipitation to PC4 and positive SIF  
532 proxy correlation in these agricultural areas (Figure 7) demonstrates the independence of GPP  
533 from precipitation in these regions., perhaps This independence implies that irrigation may be  
534 the primary driver of the under-prediction of GPP while recognising that irrigation levels are  
535 highly heterogeneous within these regions (Siebert *et al.*, 2010).

536 GPP proxies (MPI, SIF-CASA, and scaled-SIF) were as dissimilar to each other as the  
537 better performing hypotheses were to the proxies. PCA showed that the SIF based proxies  
538 had relatively higher GPP in dry, agricultural regions of the planet compared with MPI.  
539 Relatively higher SIF based GPP in cropland areas compared against MPI has been  
540 previously observed (Guanter *et al.*, 2014). This dissimilarity indicates an uncertain constraint  
541 from observations.

542 SIF is linearly related to MPI estimates of GPP at the temporal and spatial scales  
543 typically simulated by global TEMs (Guanter *et al.*, 2014; Parazoo *et al.*, 2014). SIF

544 accurately reproduces seasonality in GPP (Joiner et al., 2014), though the coefficients of the  
545 linear relationships between SIF and GPP may vary with vegetation type (Frankenberg et al.,  
546 2011; Guanter et al., 2012; Parazoo et al., 2014). By assuming that the scaled-SIF proxy  
547 follows the same linear relationship to GPP across all terrestrial ecosystems, systematic errors  
548 (epistemic uncertainties in the classification of Beven, [2016]) are likely in the scaled-SIF  
549 estimate of the global GPP distribution. However, it is also extremely likely that epistemic  
550 uncertainties are common in the system of global GPP estimation in the MPI dataset—eddy-  
551 covariance flux estimates of NEE, empirical flux partitioning to derive GPP, derivation of  
552 empirical relationships of GPP with climate variables, scaling of point estimated GPP using a  
553 gridded climate dataset. The scaled-SIF data are a relatively direct, global-scale signal from  
554 the photobiochemical photosynthetic pathway and their spatial distribution is entirely  
555 independent of the model output, in contrast with the MPI product and SIF-CASA, both of  
556 which use climate data in their calculation.

557         While the Environ\_PFT had the most data-driven and thus what we believe to be  
558 more accurate  $V_{\text{cmax},25}$  distributions, Taylor plots (Figure 5) and difference plots (Figures 6,  
559 S7, and S8) showed that their relative global GPP distributions had a larger mismatch to GPP  
560 proxies than the N limitation implementations in the northern latitudes. This difference was  
561 most apparent when compared against scaled-SIF. The latitudinal gradient in leaf N generated  
562 by the nutrient limitation implementations, and thus  $V_{\text{cmax},25}$ , redistributes global GPP towards  
563 the tropics compared with other hypotheses (Figure 2, 6 and S14), yielding global GPP  
564 distributions more similar to global GPP proxies.

565         The mismatch of the data-driven estimates of  $V_{\text{cmax},25}$  from Environ\_PFT indicates  
566 latitudinal variability in the relationship of  $V_{\text{cmax},25}$  with GPP. The reason for this mismatch is  
567 unclear. SDGVM may over-predict LAI in northern latitudes, and it may be that lower  $V_{\text{cmax}}$   
568 in nutrient limitation is compensating for high LAI. However, using a multi-scale state  
569 estimation procedure to combine GPP estimates from TEMs, SIF, and flux-towers; Parazoo et  
570 al., (2014) noted a redistribution of GPP from northern latitudes to the tropics in the  
571 optimised GPP state compared with the prior estimates from the TEMs. Similar decoupling  
572 between  $V_{\text{cmax},25}$  and GPP at high latitude has also been observed in preliminary simulations of  
573 the Community Land Model (CLM version 5.0) using satellite phenology (i.e. data-driven  
574 LAI), LUNA, and observed leaf N (Fisher, pers. Comm.). Alternatively, there may be



575 insufficient  $V_{\text{cmax}}$  data for high-latitude systems and normalising  $V_{\text{cmax}}$  to 25 °C in regions  
576 that experience these temperatures only in extreme cases and with generic temperature  
577 scaling functions could be introducing a bias in the  $V_{\text{cmax}}$  data.

578         Recent evidence has suggested that leaf phosphorus may modify, co-limit, or replace  
579 the  $V_{\text{cmax},25}$  to N relationship (Reich & Oleksyn, 2004; Domingues *et al.*, 2010; Walker *et al.*,  
580 2014a; Norby *et al.*, 2016); though the physiological link to photosynthesis is more complex.  
581 Considering P limitation either implicitly (N\_oxisolPFT) or explicitly (NP\_global) did not  
582 clearly improve the fit to the GPP proxies (compared against their N only counterparts) based  
583 on the quantitative comparison. However, a visual comparison of the difference plots  
584 suggests that the N\_oxisolPFT implementation produced the least over-all difference to GPP  
585 proxies, indicating perhaps a role for P limitation of photosynthesis in the tropics. A map of  
586 oxisols vs non-oxisols to segregate evergreen broadleaved PFTs would likely improve the  
587 simulation.

588

#### 589 *GPP trend and NBP*

590         Most importantly for projections of the global carbon cycle under environmental  
591 change, the response of GPP to global change (1901-2012) across the  $V_{\text{cmax}}$  hypotheses was  
592 different, with plant-centric acclimation hypotheses showing a lower response of GPP to  
593 increasing CO<sub>2</sub>. NBP variability over 2007-2012 was strongly related to the change in GPP  
594 over the 20<sup>th</sup> century and the 5.4% coefficient of variation in GPP to propagate through to  
595 29% variation in NBP.

596         Projecting the trajectory of land carbon uptake is the major purpose of global  
597 terrestrial ecosystem models and the 'acclimation' of  $V_{\text{cmax},25}$  to increasing CO<sub>2</sub>, and perhaps  
598 other factors of global change, predicted by these hypotheses has consequences for the  
599 projected terrestrial carbon sink. Consequences we cannot currently evaluate with data due to  
600 the difficulty in measuring GPP and terrestrial NBP, especially the 20<sup>th</sup> century trends; though  
601 coupled Earth-System models are thought to under-estimate the global carbon sink (Hoffman  
602 *et al.*, 2014).

603         Co-ord\_global and LUNA\_global predict the shallowest, and almost identical, GPP  
604 trends over the 20<sup>th</sup> century (Figure 4a). The co-ordination hypothesis (also embedded within  
605 LUNA) restricts CO<sub>2</sub> fertilisation of GPP to the effect of CO<sub>2</sub> on light-limited photosynthesis.

606 Assuming all else is equal, increasing CO<sub>2</sub> increases both the carboxylation limited  
607 photosynthetic rate,  $w_c$ , and the electron transport limited rate,  $w_j$ , but  $w_c$  is increased in  
608 greater proportion (the degree of which is dependent on the choice of model for  $w_j$ ). Thus co-  
609 ordination reduces  $V_{\text{cmax},25}$  at the higher CO<sub>2</sub> concentration to balance  $w_c$  with  $w_j$ . Thus, under  
610 co-ordination, the CO<sub>2</sub> fertilisation of GPP is primarily driven by the CO<sub>2</sub> response of light-  
611 limited photosynthesis, which is lower than the CO<sub>2</sub> response of carboxylation limited  
612 photosynthesis. The decline in  $V_{\text{cmax}}$  driven by the co-ordination hypothesis is stronger than  
613 the decline in Environ\_PFT (Figure S24) which was the only hypothesis to have an explicit  
614 reduction of  $V_{\text{cmax}}$  in response to CO<sub>2</sub>. We assumed a fixed relationship between  $J_{\text{max}}$  and  $V_{\text{cmax}}$   
615 for the implementation of co-ordination in this analysis (Eq 5). Given that these plant  
616 plasticity hypotheses are founded within the concept of optimality (Xu *et al.*, 2012; Prentice  
617 *et al.*, 2014; Wang *et al.*, 2014), the restriction of the CO<sub>2</sub> response to the smaller electron  
618 transport (light) limited under co-ordination suggests that the optimal solution would include  
619 a variable response of the  $J_{\text{max}}$  to  $V_{\text{cmax}}$  relationship to changing CO<sub>2</sub> concentration.

620

621 In summary, the analysis of multiple  $V_{\text{cmax}}$  trait scaling hypotheses on simulated GPP  
622 suggested that nutrient limitation was the more likely driver of global  $V_{\text{cmax}}$  distributions. N  
623 limitation was implemented via a relationship of decreasing leaf N with increasing soil C  
624 based on increasing costs of N uptake. Of the nutrient limitation implementations, the PFT  
625 specific relationships to leaf N that implicitly accounted for P limitation in broadleaved  
626 evergreens (Noxisol\_PFT; Kattge *et al.*, 2009) were found to most closely match the GPP  
627 proxies. Incorporating a global map of oxisols would likely help to further refine this  
628 implementation. For SDGVM and other global carbon cycle models we recommend the  
629 Noxisol\_PFT relationships to leaf N, particularly for models that can simulate N cycling or  
630 spatially dynamic leaf N. For carbon-cycle only models, the static\_PFT hypothesis did not  
631 reproduce spatial distributions of global GPP as well and we suggest that the scaled  
632 relationship of N uptake to soil C (Woodward *et al.*, 1995) without the temperature modifier  
633 could be a relatively straight forward way to implement dynamic leaf N allowing the use of  
634 the Noxisol\_PFT relationships. These recommendations are contingent on the GPP proxies  
635 used, which are uncertain. We suggest that further measurements of  $V_{\text{cmax}}$  in Boreal and Arctic

636 ecosystems, that include the  $V_{\text{cmax}}$  response to temperature in these ecosystems, will help to  
637 discriminate among alternate hypotheses.

638

639

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655

656 **Author contributions**

657 All authors contributed to the writing of the manuscript. APW conceived of the study,  
658 ran the model, analysed the data, and led the writing. APW, ML, FIW, TQ made additional  
659 developments to the SDGVM. CX contirbuted to adding the LUNA hypothesis to SDGVM.  
660 PvB derived the trait environment relationships. XY contributed the soil P dataset. JJ  
661 contributed SIF data. NM derived the land-cover datasets. MDK and TK contributed to the  
662 analysis.

663 **References**

**Ali AA, Xu C, Rogers A, Fisher RA, Wullschleger SD, Massoud EC, Vrugt JA, Muss JD, McDowell NG, Fisher JB, et al. 2016.** A global scale mechanistic model of photosynthetic capacity (LUNA V1.0). *Geoscientific Model Development* **9**: 587–606.

**Ali AA, Xu C, Rogers A, McDowell NG, Medlyn BE, Fisher RA, Wullschleger SD, Reich PB, Vrugt JA, Bauerle WL, et al. 2015.** Global-scale environmental control of plant photosynthetic capacity. *Ecological Applications* **25**: 2349–2365.

**Anav A, Friedlingstein P, Beer C, Ciais P, Harper A, Jones C, Murray-Tortarolo G, Papale D, Parazoo NC, Peylin P, et al. 2015.** Spatiotemporal patterns of terrestrial gross primary production: A review. *Reviews of Geophysics* **53**: 785–818.

**Azevedo GFC, Marengo RA. 2012.** Growth and physiological changes in saplings of *Minuartia guianensis* and *Swietenia macrophylla* during acclimation to full sunlight. *Photosynthetica* **50**: 86–94.

**Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Roedenbeck C, Arain MA, Baldocchi D, Bonan GB, et al. 2010.** Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* **329**: 834–838.

**Beven K. 2016.** Facets of uncertainty: epistemic uncertainty, non-stationarity, likelihood, hypothesis testing, and communication. *Hydrological Sciences Journal* **61**: 1652–1665.

**van Bodegom PM van, Douma JC, Verheijen LM. 2014.** A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences, USA* **111**: 13733–13738.

**van Bodegom PM, Douma JC, Witte JPM, Ordoñez JC, Bartholomeus RP, Aerts R. 2012.** Going beyond limitations of plant functional types when predicting global ecosystem–atmosphere fluxes: exploring the merits of traits-based approaches. *Global Ecology and Biogeography* **21**: 625–636.

**Bonan GB, Lawrence PJ, Oleson KW, Levis S, Jung M, Reichstein M, Lawrence DM, Swenson SC. 2011.** Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of Geophysical Research: Biogeosciences* **116**: G02014.

**Brzostek ER, Fisher JB, Phillips RP. 2014.** Modeling the carbon cost of plant nitrogen acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. *Journal of Geophysical Research: Biogeosciences* **119**: 1684–1697.

**Cernusak LA, Hutley LB, Beringer J, Holtum JAM, Turner BL. 2011.** Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. *Agricultural and Forest Meteorology* **151**: 1462–1470.

**Chen JL, Reynolds JF, Harley PC, Tenhunen JD. 1993.** Coordination theory of leaf nitrogen distribution in a canopy. *Oecologia* **93**: 63–69.

**Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, Knops J. 2002.** Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* **16**: 563–574.

**Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, et al. 2001.** Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**: 357–373.

**De Kauwe MG, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Hickler T, Jain AK, Luo Y, Parton WJ, Prentice IC, et al. 2013.** Forest water use and water use efficiency at elevated CO<sub>2</sub>: a model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biology* **19**: 1759–1779.

**De Kauwe MG, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Wang Y-P, Luo Y, Jain AK, El-Masri B, Hickler T, et al. 2014.** Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO<sub>2</sub> enrichment sites. *New Phytologist* **203**: 883–899.

**Deng X, Ye WH, Feng HL, Yang QH, Cao HL, Hui KY, Zhang Y. 2004.** Gas exchange characteristics of the invasive species *Mikania micrantha* and its indigenous congener *M. cordata* (Asteraceae) in South China. *Botanical Bulletin of Academia Sinica* **45**: 213–220.

**Domingues TF, Meir P, Feldpausch TR, Saiz G, Veenendaal EM, Schrodt F, Bird M, Djangbletey G, Hien F, Compaore H, et al. 2010.** Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment* **33**: 959–980.

**Field CB, Mooney HA. 1986.** The leaf nitrogen-photosynthesis relationship. In: Givnish TJ, ed. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press, 25–55.

**Fisher RA, Muszala S, Verteinstein M, Lawrence P, Xu C, McDowell NG, Knox RG, Koven C, Holm J, Rogers BM, et al. 2015.** Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development* **8**: 3593–3619.

**Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan S-Y. 2010.** Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation. *Global Biogeochemical Cycles* **24**: GB1014.

**Frankenberg C, Fisher JB, Worden J, Badgley G, Saatchi SS, Lee J-E, Toon GC, Butz A, Jung M, Kuze A, et al. 2011.** New global observations of the terrestrial carbon cycle from

GOSAT: Patterns of plant fluorescence with gross primary productivity. *Geophysical Research Letters* **38**: L17706.

**Friend AD, Lucht W, Rademacher TT, Keribin R, Betts R, Cadule P, Ciais P, Clark DB, Dankers R, Falloon PD, et al. 2014.** Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences, USA* **111**: 3280–3285.

**Fyllas NM, Gloor E, Mercado LM, Sitch S, Quesada CA, Domingues TF, Galbraith DR, Torre-Lezama A, Vilanova E, Ramírez-Angulo H, et al. 2014.** Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v.1). *Geoscientific Model Development* **7**: 1251–1269.

**Grime JP. 1974.** Vegetation classification by reference to strategies. *Nature* **250**: 26–31.

**Guanter L, Frankenberg C, Dudhia A, Lewis PE, Gómez-Dans J, Kuze A, Suto H, Grainger RG. 2012.** Retrieval and global assessment of terrestrial chlorophyll fluorescence from GOSAT space measurements. *Remote Sensing of Environment* **121**: 236–251.

**Guanter L, Zhang Y, Jung M, Joiner J, Voigt M, Berry JA, Frankenberg C, Huete AR, Zarco-Tejada P, Lee J-E, et al. 2014.** Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. *Proceedings of the National Academy of Sciences, USA* **111**: E1327–E1333.

**Harley PC, Thomas RB, Reynolds JF, Strain BR. 1992.** Modeling photosynthesis of cotton grown in elevated CO<sub>2</sub>. *Plant, Cell & Environment* **15**: 271–282.

**Joiner J, Guanter L, Lindstrot R, Voigt M, Vasilkov AP, Middleton EM, Huemmrich KF, Yoshida Y, Frankenberg C. 2013.** Global monitoring of terrestrial chlorophyll fluorescence from moderate-spectral-resolution near-infrared satellite measurements: methodology, simulations, and application to GOME-2. *Atmospheric Measurement Techniques* **6**: 2803–2823.

**Joiner J, Yoshida Y, Guanter L, Middleton EM. 2016.** New methods for the retrieval of chlorophyll red fluorescence from hyperspectral satellite instruments: simulations and application to GOME-2 and SCIAMACHY. *Atmospheric Measurement Techniques* **9**: 3939–3967.

**Joiner J, Yoshida Y, Vasilkov AP, Schaefer K, Jung M, Guanter L, Zhang Y, Garrity S, Middleton EM, Huemmrich KF, et al. 2014.** The seasonal cycle of satellite chlorophyll fluorescence observations and its relationship to vegetation phenology and ecosystem atmosphere carbon exchange. *Remote Sensing of Environment* **152**: 375–391.

**Jung M, Reichstein M, Margolis HA, Cescatti A, Richardson AD, Arain MA, Arneth A, Bernhofer C, Bonal D, Chen J, et al. 2011.** Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of Geophysical Research: Biogeosciences* **116**: G00J07.

**Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Boenisch G, Garnier E, Westoby M, Reich PB, Wright IJ, et al. 2011.** TRY - a global database of plant traits. *Global Change Biology* **17**: 2905–2935.

**Kattge J, Knorr W. 2007.** Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell & Environment* **30**: 1176–1190.

**Kattge J, Knorr W, Raddatz T, Wirth C. 2009.** Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* **15**: 976–991.

**Keeling CD, Piper SC, Bacastow RB, Wahlen M, Whorf TP, Heimann M, Meijer HA. 2005.** Atmospheric CO<sub>2</sub> and 13CO<sub>2</sub> exchange with the terrestrial biosphere and oceans from 1978 to 2000: observations and carbon cycle implications. In: Ehleringer JR, Cerling TE, Dearing MD, eds. *A history of atmospheric CO<sub>2</sub> and its effects on plants, animals, and ecosystems*. New York: Springer, 83–113.

**Kueppers L, Iversen C, Koven C. 2016.** Expanding use of plant trait observation in earth system models. *Eos* **97**. doi: 10.1029/2016EO049947

**Kumar J, Hoffman FM, Hargrove WW, Collier N. 2016.** Understanding the representativeness of FLUXNET for upscaling carbon flux from eddy covariance measurements. *Earth System Science Data Discussions*. doi: 10.5194/essd-2016-36

**Le Quéré C, Peters GP, Andres RJ, Andrew RM, Boden TA, Ciais P, Friedlingstein P, Houghton RA, Marland G, Moriarty R, et al. 2014.** Global carbon budget 2013. *Earth System Science Data* **6**: 235–263.

**Lemon J. 2006.** Plotrix: a package in the red light district of R. *R-News* **6**: 8–12.

**Maire V, Martre P, Kattge J, Gastal F, Esser G, Fontaine S, Soussana J-F. 2012.** The coordination of leaf photosynthesis links C and N fluxes in C3 plant species. *PLoS ONE* **7**: e38345.

**Medlyn BE, De Kauwe MG, Zaehle S, Walker AP, Duursma RA, Luus K, Mishurov M, Pak B, Smith B, Wang Y-P, et al. 2016.** Using models to guide field experiments: a priori predictions for the CO<sub>2</sub> response of a nutrient- and water-limited native Eucalypt woodland. *Global Change Biology* **22**: 2834–2851.

**Medlyn BE, Dreyer E, Ellsworth D, Forstreuter M, Harley PC, Kirschbaum MUF, Le Roux X, Montpied P, Strassmeyer J, Walcroft A, et al. 2002.** Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment* **25**: 1167–1179.



**Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler T, Jain AK, Luo Y, Parton W, et al. 2015.** Using ecosystem experiments to improve vegetation models. *Nature Climate Change* **5**: 528–534.

**Meir P, Levy PE, Grace J, Jarvis PG. 2007.** Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology* **192**: 277–287.

**Nascimento HCS, Marengo RA. 2013.** Mesophyll conductance variations in response to diurnal environmental factors in *Myrcia paivae* and *Minquartia guianensis* in Central Amazonia. *Photosynthetica* **51**: 457–464.

**Niinemets U. 1999.** Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist* **144**: 35–47.

**Norby RJ, Gu L, Haworth IC, Jensen AM, Turner BL, Walker AP, Warren JM, Weston DJ, Xu C, Winter K. 2016.** Informing models through empirical relationships between foliar phosphorus, nitrogen and photosynthesis across diverse woody species in tropical forests of Panama. *New Phytologist*. doi: 10.1111/nph.14319

**Parazoo NC, Bowman K, Fisher JB, Frankenberg C, Jones DBA, Cescatti A, Pérez-Priego Ó, Wohlfahrt G, Montagnani L. 2014.** Terrestrial gross primary production inferred from satellite fluorescence and vegetation models. *Global Change Biology* **20**: 3103–3121.

**Pavlick R, Drewry DT, Bohn K, Reu B, Kleidon A. 2013.** The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences* **10**: 4137–4177.

**Picard G, Woodward FI, Lomas MR, Pellenq J, Quegan S, Kennedy M. 2005.** Constraining the Sheffield dynamic global vegetation model using stream-flow measurements in the United Kingdom. *Global Change Biology* **11**: 2196–2210.

**Poulter B, MacBean N, Hartley A, Khlystova I, Arino O, Betts R, Bontemps S, Boettcher M, Brockmann C, Defourny P, et al. 2015.** Plant functional type classification for earth system models: results from the European Space Agency’s Land Cover Climate Change Initiative. *Geoscientific Model Development* **8**: 2315–2328.

**Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ. 2014.** Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecology Letters* **17**: 82–91.

**R Core Development Team. 2011.** *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

**Read DJ. 1991.** Mycorrhizas in ecosystems. *Experientia* **47**: 376–391.

**Reich PB. 2014.** The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

**Reich PB, Oleksyn J. 2004.** Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences, USA* **101**: 11001–11006.

**Rogers A. 2014.** The use and misuse of  $V_{c,max}$  in Earth System Models. *Photosynthesis Research* **119**: 15–29.

**Rogers A, Medlyn BE, Dukes JS, Bonan G, von Caemmerer S, Dietze MC, Kattge J, Leakey ADB, Mercado LM, Niinemets Ü, et al. 2017.** A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytologist* **213**: 22–42.

**Sargsyan K, Safta C, Najm HN, Debusschere BJ, Ricciuto D, Thornton P. 2014.** Dimensionality reduction for complex models via bayesian compressive sensing. *International Journal for Uncertainty Quantification* **4**: 63–93.

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

**Siebert S, Burke J, Faures JM, Frenken K, Hoogeveen J, Döll P, Portmann FT. 2010.** Groundwater use for irrigation – a global inventory. *Hydrology and Earth System Sciences* **14**: 1863–1880.

**Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P, et al. 2008.** Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology* **14**: 2015–2039.

**Smith TM, Shugart HH, Woodward FI (Eds.). 1998.** *Plant functional types: their relevance to ecosystem properties and global change*. Cambridge: Cambridge University Press.

**Taylor KE. 2001.** Summarizing multiple aspects of model performance in a single diagram. *Journal of Geophysical Research: Atmospheres* **106**: 7183–7192.

**Verheijen LM, Aerts R, Brovkin V, Cavender-Bares J, Cornelissen JHC, Kattge J, van Bodegom PM. 2015.** Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology* **21**: 3074–3086.

**Verheijen LM, Brovkin V, Aerts R, Bönisch G, Cornelissen JHC, Kattge J, Reich PB, Wright IJ, van Bodegom PM. 2013.** Impacts of trait variation through observed trait–climate relationships on performance of an Earth system model: a conceptual analysis. *Biogeosciences* **10**: 5497–5515.

**Walker AP, Beckerman AP, Gu L, Kattge J, Cernusak LA, Domingues TF, Scales JC, Wohlfahrt G, Wullschleger SD, Woodward FI. 2014a.** The relationship of leaf photosynthetic traits –  $V_{c,max}$  and  $J_{max}$  – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution* **4**: 3218–3235.

**Walker AP, Hanson PJ, De Kauwe MG, Medlyn BE, Zaehle S, Asao S, Dietze M, Hickler T, Huntingford C, Iversen CM, et al. 2014b.** Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO<sub>2</sub> enrichment experiments: Model performance at ambient CO<sub>2</sub> concentration. *Journal of Geophysical Research: Biogeosciences* **119**: 937–964.

**Wang H, Prentice IC, Davis TW. 2014.** Biophysical constraints on gross primary production by the terrestrial biosphere. *Biogeosciences* **11**: 5987–6001.

**van de Weg MJ, Meir P, Grace J, Ramos GD. 2011.** Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia* **168**: 23–34.

**Woodward FI, Cramer W. 1996.** Plant functional types and climatic change: Introduction. *Journal of Vegetation Science* **7**: 306–308.

**Woodward FI, Lomas MR. 2004.** Vegetation dynamics - simulating responses to climatic change. *Biological Reviews* **79**: 643–670.

**Woodward FI, Smith TM. 1994.** Global photosynthesis and stomatal conductance - modeling the controls by soil and climate. In: Callow, J. A., ed. *Advances in Botanical Research. Volume 20*. 1–41.

**Woodward FI, Smith TM. 1995.** Predictions and measurements of the maximum photosynthetic rate, A<sub>max</sub>, at the global scale. In: Schulze E-D, Caldwell MM, eds. Springer Study Edition. *Ecophysiology of Photosynthesis*. Springer Berlin Heidelberg, 491–509.

**Woodward FI, Smith TM, Emanuel WR. 1995.** A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles* **9**: 471–490.

**Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

**Wullschleger SD, Epstein HE, Box EO, Euskirchen ES, Goswami S, Iversen CM, Kattge J, Norby RJ, Bodegom V, M P, et al. 2014.** Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany* **114**: 1–16.

**Xu C, Fisher R, Wullschleger SD, Wilson CJ, Cai M, McDowell NG. 2012.** Toward a mechanistic modeling of nitrogen limitation on vegetation dynamics. *PLoS ONE* **7**: e37914.

**Yang X, Post WM, Thornton PE, Jain AK. 2014.** Global Gridded Soil Phosphorus Distribution Maps at 0.5-degree Resolution. doi: 10.3334/ORNLDAAC/1223

**Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T, Luo Y, Wang Y-P, El-Masri B, Thornton P, et al. 2014.** Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment studies. *New Phytologist* **202**: 803–822.

**Zaehle S, Sitch S, Smith B, Hatterman F. 2005.** Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles* **19**: GB3020.

## Figure Captions

664

665 Figure 1. Mean growing season top-leaf  $V_{\text{cmax},25}$  ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) over the period 2007-2012 for  
666 the nine implementations of the four  $V_{\text{cmax}}$  trait-scaling hypotheses. Growing season defined  
667 as periods during which LAI was greater than one. Values are reported prior to scaling of  
668  $V_{\text{cmax}}$  by water-stress or leaf-age.

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670 Figure 2. Mean annual GPP ( $\text{gC m}^{-2}\text{y}^{-1}$ ) for the period 2007-2012 for the nine  
671 implementations of the four  $V_{\text{cmax}}$  trait-scaling hypotheses and the three global GPP proxies.  
672 Global mean annual GPP shown in each panel ( $\text{PgC}$ ).

673

674 Figure 3. Mean annual zonal GPP ( $\text{PgC}$ ) over the period 2007-2012 for three of the  $V_{\text{cmax}}$   
675 trait-scaling implementations in combination with the three temperature scaling assumptions.

676

677 Figure 4. Variability in GPP trends and NBP for the nine implementations of the four  $V_{\text{cmax}}$   
678 trait-scaling hypotheses. (a) Trends in the absolute change in global GPP over the period  
679 1901-2012; and (b) the relationship between mean annual NBP 2007-2012 and the change in  
680 GPP 1901-2012 across the nine hypotheses.

681

682 Figure 5. Taylor plots of GPP (2007-2012) for the nine implementations of the four  $V_{\text{cmax}}$   
683 trait-scaling hypotheses compared against the three GPP proxies: (a) MPI, (b) SIF-CASA, (c)  
684 scaled-SIF; and (d) including the two additional temperature scaling hypotheses (modA and  
685 tacc) for N\_global, N\_PFT, LUNA\_global and co-ord\_global. Taylor plots compare datasets  
686 against a reference dataset using correlation (grey radial isolines), standard deviation (blue  
687 circular isolines, zero at the origin), and root mean difference (green circular isolines, zero at  
688 the reference dataset on the x-axis).

689

690 Figure 6. Difference plot of GPP simulated by the nine implementations of the four  $V_{\text{cmax}}$   
691 trait-scaling hypotheses minus the scaled-SIF GPP proxy.

692

693 Figure 7. Principle components analysis of the nine implementations of the four  $V_{\text{cmax}}$  trait-  
694 scaling hypotheses with the three GPP proxies and three climatic variables: precipitation,  
695 temperature, and short-wave radiation. Loadings of variables on (a) PC1 and PC2, (b) PC3  
696 and PC4; maps of (c) PC1 pattern (d) PC2 pattern (e) PC3 pattern, and (f) PC4 pattern. Break  
697 points on the colour scale are at quantiles (0.025, 0.1, 0.2, 0.35, 0.65, 0.8, 0.9, 0.975) in the  
698 gridpoint scores on each PC to give even representation of the data.  
699

700 Table 1. Summary of  $V_{c_{max,25}}$  and  $V_{c_{max}}$  temperature scaling hypotheses.

| Hypothesis                             | Label               | Specific method                     | PFT specific  | Description  | Reference                             | Papers/Models               | Dataset                               |
|--|---------------------|-------------------------------------|---------------|--|---------------------------------------|-----------------------------|---------------------------------------|
| Static                                 | static_PFT          | Static                              | Y             | Augmented TRY database means   | Verheijen et al., 2015                | Most CMIP5 models           | Literature search augmented TRY       |
| Nutrient limitation                    | Ntemp_global        | empirical f(Nu)                     | N             |  | Woodward et al., 1995                 | Original SDGVM              | Woodward et al., 1995                 |
|  | N_global            | empirical f(Na)                     | N             | Power law  | Walker et al., 2014                   |                             | Literature search Walker et al., 2014 |
|  | NP_global           | empirical f(Na,Pa)                  | N             | Power law including leaf phosphorus  | Walker et al., 2014                   |                             | Literature search Walker et al., 2014 |
|  | N_PFT               | empirical f(Na)                     | Y             | Linear from TRY database   | Kattge et al., 2009                   | O-CN, other N cycle models, | TRY                                   |
|  | N_oxisolPFT         | empirical f(Na)                     | Y             | As above but with oxisol relationship for evergreen broadleaf PFT                          | Kattge et al., 2009                   |                             | TRY                                   |
| Environmental filtering                | Environ_PFT         | empirical f(env.)                   | Y             | Augmented TRY relationship to ...  | Verheijen et al., 2015                |                             | Literature search augmented TRY       |
| Plant plasticity                       | Co-ord_global       | Theoretical f(Q, T, VDP)            | N             | $V_{c_{max}}$ adjusted so $w_c = w_j$ given mean environment over the past 30 days         | Chen et al., 1993; Maire et al., 2012 | First principles Wang et al | na                                    |
| Plant plasticity & nutrient limitation | LUNA_global         | 4. Theoretical f(Na, Q, T, RH)      | N             | Constrained optimisation of leaf N allocation given mean environment over the past 30 days | Xu et al., 2012; Ali et al., 2016     | CLM5.0                      | Literature search Ali et al., 2015    |
|  | Temperature scaling |                                     |               |  |                                       |                             |                                       |
| Static                                 | *                   | SDGVM default                       | N             | Saturating exponential   |                                       | SDGVM                       |                                       |
| Static                                 | *_modA              | Modified Arrhenius                  | Y             | Temperature optimum  | Medlyn et al., 2002                   |                             |                                       |
| Plant plasticity                       | *_tacc              | Modified Arrhenius with acclimation | Y (modA only) | Temperature optimum varies with growth temperature   | Kattge & Knorr, 2007                  |                             |                                       |

701 Nu—N uptake, Na—N per unit leaf area, Pa—P per unit leaf area, Q—incident PAR per unit

702 leaf area, T—leaf temperature, VPD—vapour pressure deficit, RH—relative humidity. \*

703 represents the label for one of four Vcmax scaling hypotheses (N\_global, N\_PFT,  
704 LUNA\_global, or Co-ord\_global) used in conjunction with these three temperature scaling  
705 hypotheses.  
706



707 Table 2. Carbon cycle variables for the nine Vcmax scaling hypotheses (means over the  
 708 period 2007-2012). Net primary productivity, NPP; soil carbon stocks, Csoil; vegetation  
 709 carbon stocks, Cveg; total terrestrial carbon stocks, Ctotal; standard deviation, sd; coefficient  
 710 of variation, CV. All variables are in gC m<sup>-2</sup> y<sup>-1</sup>.

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|               | GPP          | NPP         | NBP         | Csoil         | Cveg         | Ctotal        |
|---------------|--------------|-------------|-------------|---------------|--------------|---------------|
| static_PFT    | 127.8        | 73.4        | 1.7         | 1619.8        | 777.7        | 2397.5        |
| Ntemp_global  | 128.2        | 71.1        | 2.9         | 1009.5        | 768.0        | 1777.5        |
| N_global      | 121.7        | 66.8        | 2.1         | 1304.6        | 680.9        | 1985.5        |
| N_PFT         | 116.5        | 64.9        | 1.9         | 1285.6        | 581.8        | 1867.4        |
| N_oxisolPFT   | 110.6        | 62.5        | 1.6         | 1270.9        | 517.4        | 1788.3        |
| NP_global     | 118.0        | 64.1        | 1.9         | 1289.6        | 694.2        | 1983.8        |
| LUNA_global   | 108.1        | 60.9        | 1.2         | 1349.2        | 558.4        | 1907.7        |
| environ_PFT   | 118.1        | 66.2        | 1.9         | 1253.1        | 781.2        | 2034.3        |
| co-ord_global | 119.3        | 69.6        | 1.1         | 1494.9        | 714.3        | 2209.2        |
| <b>mean</b>   | <b>118.7</b> | <b>66.6</b> | <b>1.8</b>  | <b>1319.7</b> | <b>674.9</b> | <b>1994.6</b> |
| <b>sd</b>     | <b>6.4</b>   | <b>3.9</b>  | <b>0.5</b>  | <b>158.8</b>  | <b>94.0</b>  | <b>189.6</b>  |
| <b>CV (%)</b> | <b>5.4</b>   | <b>5.8</b>  | <b>27.3</b> | <b>12.0</b>   | <b>13.9</b>  | <b>9.5</b>    |

724 Supplemental Material  
725  
726 Figure S1. Temperature responses of  $V_{\text{cmax}}$ .  
727 Figure S2-S4. Climate data used to run the model.  
728 Figure S5-S12. Land-cover data used to run the model.  
729 Figure S13. Zonal plot of  $V_{\text{cmax},25}$ .  
730 Figure S14. Zonal plot of GPP.  
731 Figure S15. Global GPP for various  $V_{\text{cmax}}$  temperature scaling assumptions.  
732 Figure S16. 20<sup>th</sup> and 21<sup>st</sup> change in GPP for various  $V_{\text{cmax}}$  temperature scaling assumptions.  
733 Figure S17. GPP observation proxies.  
734 Figure S18. Difference plot of model GPP to MPI GPP proxy.  
735 Figure S19. Difference plot of model GPP to SIF-CASA GPP proxy.  
736 Figure S20. Variance explained by each principal component.  
737 Figure S21-S23. Modelled relationships between leaf N and  $V_{\text{cmax},25}$  with soil carbon.  
738 Figure S24. 20<sup>th</sup> and 21<sup>st</sup> change in modelled  $V_{\text{cmax},25}$ .  
739 Figure S25. 20<sup>th</sup> and 21<sup>st</sup> change in modelled LAI.  
740  
741 Notes S1. Additional methods description.  
742  
743 Table S1. Metrics for Taylor plots.  
744