

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

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48 **Summary**

- 49 • The maximum carboxylation rate of photosynthesis (V_{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_{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_{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_{cmax}) and the maximum electron transport rate (J_{max}), and terrestrial
83 carbon cycle models are highly sensitive to these parameters (Zaehle *et al.*, 2005; Bonan *et al.*,
84 2011; Sargsyan *et al.*, 2014; Rogers, 2014; Rogers *et al.*, 2017). Many methods are used
85 across TBMs to calculate V_{cmax} and J_{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_{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_{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_{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_{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_{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_{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_{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_{cmax} scaling hypothesis—PFT, nutrient limitation, environmental filtering, and
167 plant plasticity—for V_{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 $V_{c_{max,25}}$ 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 $V_{c_{max}}$
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:

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

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 $V_{c_{max,25}}$ 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 $V_{c_{max,25}}$ a function of $V_{c_{max,25}}$ 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:

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

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 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_{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 (PepC₂₅) 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_{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):

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

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

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; 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 CO₂ 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_{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_{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 y^{-1} (Figure 2; Table 2). The ensemble
348 mean \pm s.d. annual GPP was 118.7 ± 6.4 PgC 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⁻¹. 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⁻¹. The inclusion of P as an additional limiting factor resulted in lower global GPP
356 by 3.7 and 5.9 PgC y⁻¹ 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⁻¹. The constrained optimisation of functional leaf N allocation (LUNA
361 hypothesis) yielded the lowest GPP at 108.1 PgC y⁻¹.

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⁻¹). 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 CO₂ and changing climate (Figure 4a). Ntemp_global
371 resulted in the strongest change in GPP over the 20th 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_{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_{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_{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 y^{-1} (mean 118.7 ± 6.4 PgC 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 y^{-1} , mean 145.6 ± 12.6 PgC 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_{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_{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_{cmax} datasets are only sparsely represented and one of the most
478 comprehensive global V_{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 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_{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_{cmax} data for high-latitude systems and normalising V_{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_{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_{cmax} hypotheses was
592 different, with plant-centric acclimation hypotheses showing a lower response of GPP to
593 increasing CO_2 . NBP variability over 2007-2012 was strongly related to the change in GPP
594 over the 20th 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_2 , 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 20th 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 20th century (Figure 4a). The co-ordination hypothesis (also embedded within
605 LUNA) restricts CO_2 fertilisation of GPP to the effect of CO_2 on light-limited photosynthesis.

606 Assuming all else is equal, increasing CO₂ 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 CO₂ concentration to balance w_c with w_j . Thus, under
610 co-ordination, the CO₂ fertilisation of GPP is primarily driven by the CO₂ response of light-
611 limited photosynthesis, which is lower than the CO₂ response of carboxylation limited
612 photosynthesis. The decline in V_{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_{cmax} in response to CO₂. We assumed a fixed relationship between J_{max} and V_{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 CO₂ 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_{max} to V_{cmax} relationship to changing CO₂ concentration.

620

621 In summary, the analysis of multiple V_{cmax} trait scaling hypotheses on simulated GPP
622 suggested that nutrient limitation was the more likely driver of global V_{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_{cmax} in Boreal and Arctic

636 ecosystems, that include the V_{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.

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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_{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_{cmax} by water-stress or leaf-age.

669

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_{cmax} trait-scaling hypotheses and the three global GPP proxies.
672 Global mean annual GPP shown in each panel (PgC).

673

674 Figure 3. Mean annual zonal GPP (PgC) over the period 2007-2012 for three of the V_{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_{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_{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_{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_{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 specifi c	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
	Static	Temperature scaling	*	SDGVM default			SDGVM
Static	*_modA	Modified Arrhenius	Y	Saturating exponential	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⁻² y⁻¹.

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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
mean	118.7	66.6	1.8	1319.7	674.9	1994.6
sd	6.4	3.9	0.5	158.8	94.0	189.6
CV (%)	5.4	5.8	27.3	12.0	13.9	9.5

724 Supplemental Material
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726 Figure S1. Temperature responses of V_{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_{cmax} temperature scaling assumptions.
732 Figure S16. 20th and 21st change in GPP for various V_{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. 20th and 21st change in modelled $V_{\text{cmax},25}$.
739 Figure S25. 20th and 21st change in modelled LAI.
740
741 Notes S1. Additional methods description.
742
743 Table S1. Metrics for Taylor plots.
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