Putting land ecosystem models on firmer foundations

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with contributions from the next-generation model development group:

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The current state of the art

- Future projections diverge wildly
- Many land properties are not well captured
- Major differences in process representations...
  - historical legacy from the 1980s
  - incorrect assumptions
  - lack of attention to observations
The current state of the art

- Future projections diverge wildly
- Many land properties are not well captured
- Major differences in process representations...
  - Vast increase in observations since the 1980s, including:
    - CO$_2$ and other tracer concentrations
    - local CO$_2$ and $\lambda E$ fluxes
    - plant trait data compilations, incl. isotopes, photosynthesis
    - raised-CO$_2$ experiments (esp. FACE)
    - EO satellites
    - palaeodata
Models are going nowhere (fast!)

- Neither coherent nor transparent
- “Improvement” = adding new processes and parameters
  - instead of re-examining the old ones
- Observations = “benchmarking” model outputs
  - instead of exploring and testing model processes
21st century land C uptake in models: no agreement and no convergence

Prentice et al. (2015) Atmospheric Chemistry and Physics
Primary production and latent heat flux in models: mostly outside the accepted ranges

Prentice et al. (2015) Atmospheric Chemistry and Physics
CO₂ uptake:

too little – most ESMs overpredict present CO₂

Hoffman et al. (2014) Journal of Geophysical Research
Plotting $\gamma_{LT}$ against $\gamma_{IAV}$ reveals the emergent constraint identified by Cox et al. [2013], and we do this for both the Historical simulations and the 1%COU simulations (Figure 5) to test for robustness. In both cases, there is evidence of a linear relationship between $\gamma_{LT}$ and $\gamma_{IAV}$, which holds for all the models apart from MPI-ESM-LR. This model shows a surprising net negative correlation between variations in soil respiration and temperature, most likely due to a strong suppression of soil respiration under reducing soil moisture, which overwhelms the usual increase in soil respiration with warming [Ciais et al., 2005; Reichstein et al., 2007; Zaehle et al., 2010]. As a result, MPI-ESM-LR has unusually high soil carbon in dry regions, which is vulnerable to climate change (Figure 5a). It therefore seems that MPI-ESM-LR does not fit on the $\gamma_{IAV}$-$\gamma_{LT}$ correlation line (Figure 5a) as its short-term response is driven by different processes (the suppression of heterotrophic

CO$_2$ seasonal cycle in the northern atmosphere: 
*amplitude predicted poorly, amplification too small*

Figure 2. ASC in 2009–2010 compared to percentage change in ASC from 1958–1961 to 2009–2010 for aircraft observations (black square), MsTMIP models (colored markers), and CMIP5 models for TM3 only (grey markers) (revised from [Graven et al., 2013]). Grey shading is observational uncertainty [Graven et al., 2013].

Capture the phase of the CO$_2$ seasonal cycle (Figure S3a). The primary driver of the increase in modeled ASC is CO$_2$ (Figure 4). Coupled carbon-nitrogen cycle (C-N) models have among the smallest changes in ASC and the weakest CO$_2$-driven increases. The small CO$_2$-driven ASC increase in C-N models is likely due to N limitation, as ASC further increases in simulations when time-varying N deposition is included. LPJwsl is the only model that has a fractional increase in ASC within the observational uncertainty (47%) (Figure 2), but its absolute ASC and ASC change are much too small (Figure 1). The ASC change in the MsTMIP models is similar to the CMIP5 models [Graven et al., 2013, Figure 2], although MsTMIP models tend to have smaller 2009–2010 amplitudes.

3.2. Vegetation Greenness

Models are generally able to reproduce the observed interannual variability in GS-fAPAR and its increase of 0.02 (8.7%) between 30 and 90$^\circ$N from 1982 to 2010 (Figures 4b and S3b). Observed and modeled greening was due to an increase in leaves per unit area, rather than vegetated area. Only ISAM showed an increase in vegetated area. All models show that greening is driven by climate (Figure 4b), and models perform best in arctic and boreal regions where greening trends have been driven by increasing temperatures [Piao et al., 2006] (Figure S1). There is little influence on the overall greening trend from LUC, CO$_2$, and N deposition. These drivers may be of more importance at lower latitudes where models do not match observed trends well (Figure S1) and where greening trends depend more on how vegetation is represented in models [Eastman et al., 2013; Murray-Tortarolo et al., 2013; Zhu et al., 2016].

3.3. Terrestrial Carbon Fluxes

3.3.1. NEP

The amplitude of NEP varies from less than 1 Pg C yr$^{-1}$ to more than 5 Pg C yr$^{-1}$, consistent with previous studies showing MsTMIP models have high intermodel variability in NEP, as well as in its constituent fluxes, gross primary production, and ecosystem respiration [Huntzinger et al., 2013; Zscheischler et al., 2014; Schwalm et al., 2015]. NEP amplitude generally increased (Figure 3b), as shown previously for MsTMIP [Ito et al., 2016] and TRENDY [Zhao et al., 2016]. NEP amplitude is well correlated to the simulated ASC across the models; $r^2 = 0.95$ (Figure 3a). There is also a good correlation between NEP amplitude change and ASC change (Figure 3b), though somewhat weaker ($r^2 = 0.70$), which may be due to additional influences on ASC change from fluxes south of 30$^\circ$N.

Figure 3b also shows the optimized flux of NEP, from Graven et al. [2013], where NEP amplitude in arctic, boreal, and temperate regions were adjusted to best match the pattern of observed ASC change in aircraft and surface data. The optimized increase in NEP amplitude from Graven et al. [2013] is larger than any modeled increase, but it lies within the uncertainty of the model regression line, indicating that the relationship between ASC and NEP amplitude change is similar.
Responses of weekly GPP to PAR, vpd, T

OBS

TF Keenan et al. (in prep.)
Responses of weekly GPP to PAR, vpd, T

TF Keenan et al. (in prep.)
We can (and should) do much better!

- Formulate hypotheses about individual processes
- Make quantitative predictions
- Use data extensively, to provide tests
We can (and should) do much better!

- Formulate hypotheses about individual processes
- Make quantitative predictions
- Use data extensively, to provide tests
  (normal scientific method!)
What hypotheses?

- Natural selection => source of predictability in biological systems
- Optimality criteria => testable predictions of *acclimation* and *adaptation*...
- ...and *simpler* process representations, fewer parameters, analytical tractability
What controls the $c_i: c_a$ ratio ($\chi$)?

- CO$_2$ inside the leaf ($c_i$) $<$ CO$_2$ in the air ($c_a$)
- Ratio is the “exchange rate” (carbon gain vs water loss)
- Indexed by the stable carbon isotope ratio ($\delta^{13}$C)
- Least-cost hypothesis:
  - $\chi$ minimizes the sum of the *unit costs* of maintaining capacities for carbon gain and water loss

Least-cost hypothesis for the regulation of $\chi$

Problem: to minimize

$$a \ (E/A) + b \ (V_{\text{cmax}}/A)$$

leading to

$$\chi \approx \xi / (\xi + \sqrt{D})$$

where

$$\xi = \sqrt{(bK/1.6a)}$$

$$K = K_C \ (1 + O/K_O)$$

..............................

$$a = r_s h^2 \rho_s \eta / 2(\Delta \psi) k_s \rho_w$$

$$b = \text{constant}$$

Prentice et al. (2014) Ecology Letters
Consequences

• $\chi$ is (almost) independent of $c_a$ and PAR, but responds to other drivers:
  
  $\uparrow$ with growth temperature ($K_c, K_o, \eta$)
  $\downarrow$ with vapour pressure deficit ($D$)
  $\downarrow$ with elevation ($O, D$)
response of $\ln \{\chi/(1 - \chi)\}$ to drivers

<table>
<thead>
<tr>
<th></th>
<th>predicted</th>
<th>from $\delta^{13}\text{C}$ data</th>
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<tbody>
<tr>
<td>temperature (K)</td>
<td>0.054</td>
<td>0.052 $\pm$ 0.006</td>
</tr>
<tr>
<td>$\ln \text{vpd}$</td>
<td>$-0.5$</td>
<td>$-0.55 \pm 0.06$</td>
</tr>
<tr>
<td>elevation (km)</td>
<td>$-0.08$</td>
<td>$-0.11 \pm 0.03$</td>
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Wang et al. (2017) *Nature Plants*
Observed $\chi$

Predicted $\chi$

Evergreen broadleaf tree
Deciduous broadleaf tree
Evergreen needleleaf tree
Deciduous needleleaf tree
Savanna tree
Shrub
C3 grass

Wang et al. (2017) Nature Plants
What controls $V_{\text{cmax}}$?

- Capacity for CO$_2$ fixation – master variable for land carbon cycling
- Co-ordination hypothesis: $V_{\text{cmax}}$ is just sufficient to use the light absorbed by the leaf (no more, no less)

Chen et al. (1993) *Oecologia*
Dewar (1996) *Annals of Botany*
Maire et al. (2012) *PLOS One*
Co-ordination hypothesis for the regulation of $V_c\text{max}$

Equate the enzyme- and light-limited rates of photosynthesis (for average daytime absorbed PAR, $I_{abs}$)

$$A_C = V_{c\text{max}} (c_i - \Gamma^*) / (c_i + K)$$

$$A_J \approx \phi_0 I_{abs} (c_i - \Gamma^*) / (c_i + 2\Gamma^*)$$

leading to

$$V_{c\text{max}} \approx \phi_0 I_{abs} (c_i + K) / (c_i + 2\Gamma^*)$$

Dong et al. (2017) Biogeosciences
Consequences

• $V_{cmax}$ varies inversely with $\chi$, and also depends on light and temperature:

  ↑ in proportion to PAR ($I_{abs}$)

  ↑ with growth temperature ($K >> \Gamma*$), but less steeply than the “instantaneous” response shown by lab measurements
Leaf respiration ($R_d$) and $V_{cmax}$ versus growth temperature

H Wang et al. (in prep.)
Global pattern in $V_{cmax}$

Slope: 1.00 [0.90, 1.12]
Intercept: -4.71 [-8.62, -1.21]
$r^2 = 0.63; P < 0.001$

N Smith et al.
(in prep.)
Some other predictions (also correct)

- higher $V_{c_{\text{max}}}$ in dry environments
- higher $V_{c_{\text{max}}}$ at high elevations
  first observed: Körner & Diemer (1987) *Functional Ecology*
  explained: Wang *et al.* (2017) *New Phytologist*
- slightly lower $V_{c_{\text{max}}}$ at elevated $c_{a}$ (‘down-regulation’)

•
What controls the light use efficiency (LUE) of gross primary production (GPP)?

- GPP is total CO$_2$ uptake by plants – the basis for all life on land
- Monteith equation:
  \[ \text{GPP} = \text{LUE} \times f\text{APAR} \times \text{IPAR} \]
  underlies “LUE models”, with fAPAR from satellite data
- We can *explain* this as a consequence of the co-ordination hypothesis
  ....and *predict* it as well....
A universal LUE model for GPP

\[ A_J = \varphi_0 I_{abs} m \sqrt{1 - \left( \frac{c^*}{m} \right)^2} \]

\[ m = \frac{c_a - \Gamma^*}{c_a + 2\Gamma^* + 3\Gamma^*} \frac{1.6D\eta^*}{\sqrt{\beta(K + \Gamma^*)}} \]

where

\[ \varphi_0 = 0.085 \]
\[ c^* = 0.41 \]
\[ \beta = 146 \]

Wang et al. (2017) Nature Plants
Global data-model comparison of monthly GPP

\[ r = 0.7418, \quad \text{RMSE} = 69.442 \]

Wang et al. (2017) Nature Plants
Data-model comparison of CO$_2$ effects

Comparison with Ainsworth & Long’s (2005) meta-analysis of FACE experiments (≈ 200 ppm CO$_2$ enhancement):

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<tr>
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<th>meta-analysis</th>
<th>model</th>
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<tbody>
<tr>
<td>Light use efficiency</td>
<td>12.2 ± 9 %</td>
<td>15.2 %</td>
</tr>
<tr>
<td>Water use efficiency</td>
<td>54.3 ± 17 %</td>
<td>55 %</td>
</tr>
<tr>
<td>Stomatal conductance</td>
<td>−20.0 ± 3 %</td>
<td>−15.0 %</td>
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Wang et al. (2017) Nature Plants
Immediate, practical spin-offs

- We can predict LUE:
  - with *no* “plant functional types” (except $C_3$ and $C_4$)
  - *no* discontinuities
  - a realistic *response to CO$_2$
  - in contrast with existing LUE models, e.g. MODIS GPP

- ESA project: [https://terra-p.vito.be/](https://terra-p.vito.be/)
  - new GPP monitoring system

- Collaboration with ECMWF
  - new carbon cycle re-analysis
An ambitious, longer-term research programme

- Foundations for modelling NPP, biomass production, C allocation => green vegetation cover
- Explanations for the distributions of plant life forms
- Model-based approach to competition and co-existence => accounting for functional diversity in a next-generation model