

Using ecosystem experiments to improve vegetation models

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Ecosystem responses to rising CO₂ concentrations are a major source of uncertainty in climate change projections. Data from ecosystem-scale Free-Air CO₂ Enrichment (FACE) experiments provide a unique opportunity to reduce this uncertainty. The recent FACE Model-Data Synthesis project aimed to use the information gathered in two forest FACE experiments to assess and improve land ecosystem models. A new 'assumption-centred' model intercomparison approach was used, in which participating models were evaluated against experimental data based on the ways in which they represent key ecological processes. By identifying and evaluating the main assumptions causing differences among models, the assumption-centred approach produced a clear roadmap for reducing model uncertainty. Here, we explain this approach and summarize the resulting research agenda. We encourage the application of this approach in other model intercomparison projects to fundamentally improve predictive understanding of the Earth system.

The response of the terrestrial biosphere to increasing atmospheric CO₂ concentration (C_a) is a major uncertainty in models projecting future climate change, because of the critical feedback between terrestrial ecosystem carbon (C) cycling and the atmosphere^{1–3}. Current Earth system models disagree strongly on the size of this feedback². This disagreement results from differences in the projected increase of plant production owing to CO₂ fertilization, including its interactions with terrestrial nitrogen (N)^{4–6} and phosphorus⁷ cycles, as well as differences in the turnover times of C in terrestrial ecosystems⁸. These differences among models imply that our predictive understanding of the effects of C_a on terrestrial C storage remains very low.

FACE experiments aim to investigate how terrestrial ecosystems respond to elevated atmospheric CO₂ concentration (eC_a). In general, FACE experiments are ecosystem-scale, long-term, multi-investigator experiments that provide an extraordinarily rich source of data on plant and soil processes mediating ecosystem-level responses to eC_a (refs 9,10). However, the full richness of these experiments has rarely been exploited to constrain model uncertainty, with model outputs typically only being compared against the response of net primary production (for example, refs 11–13).

The FACE Model-Data Synthesis (FACE-MDS) project¹⁴ aimed to benefit from the wide range of complementary data sets available from these experiments to better constrain eC_a responses in models. To do so, we followed an 'assumption-centred' approach, in which we studied the underlying assumptions that models use to represent key ecosystem processes, and evaluated which assumptions best represented the experimental data. We used 11 process-based models, including four stand-scale ecosystem models (DAYCENT¹⁵, ED2¹⁶, GDAY¹⁷ and TECO¹⁸), five land surface models (CABLE¹⁹, CLM4²⁰, EALCO²¹, ISAM²² and O-CN²³) and two dynamic vegetation models (LPJ-GUESS²⁴ and SDGVM²⁵). These models were compared with data from two

temperate FACE experiments on established forest plantations: the Duke FACE experiment on *Pinus taeda*²⁶ and the Oak Ridge National Laboratory (ORNL) FACE experiment on *Liquidambar styraciflua*²⁷ (Fig. 1). These two experiments have the advantage of being stand-level, ecosystem experiments in established forests that are readily comparable with ecosystem-scale models. Both experiments ran for more than ten years, during which time data were collected on many aspects of ecosystem function.

The major processes we studied included net primary production (NPP) and N cycling²⁸, water use and water-use efficiency (WUE)²⁹, and allocation and turnover³⁰. The two experiments demonstrated contrasting responses for each of these processes. The eC_a stimulation of NPP at Duke varied among FACE rings depending on N availability, but the site-average response remained high throughout the course of the experiment^{26,31}. C allocation patterns did not change greatly, so the increase in NPP led to higher leaf area index (LAI)³² and higher vegetation C storage at the end of the experiment. There was little change in total plant water use³³. In contrast, at ORNL, the initial stimulation of NPP by eC_a declined over time owing to developing nutrient limitations²⁷, and allocation shifted strongly belowground³⁴, resulting in no change in LAI or vegetation C storage but a reduction in plant water use³⁵. These contrasts between the experiments heightened the challenge for the models to simulate them accurately.

The methods and results from the project are fully reported in refs. 14, 28–30, and project data^{36,37} are available from <http://cdiac.ornl.gov/face>. The goal of this Perspective is to explain the approach that we took to the intercomparison and to demonstrate the success of this approach by synthesizing our results into a clear research agenda for reducing model uncertainty.

The assumption-centred approach

Model intercomparisons against data often use a 'benchmarking' approach³⁸ (Fig. 2a), in which models are compared against a suite

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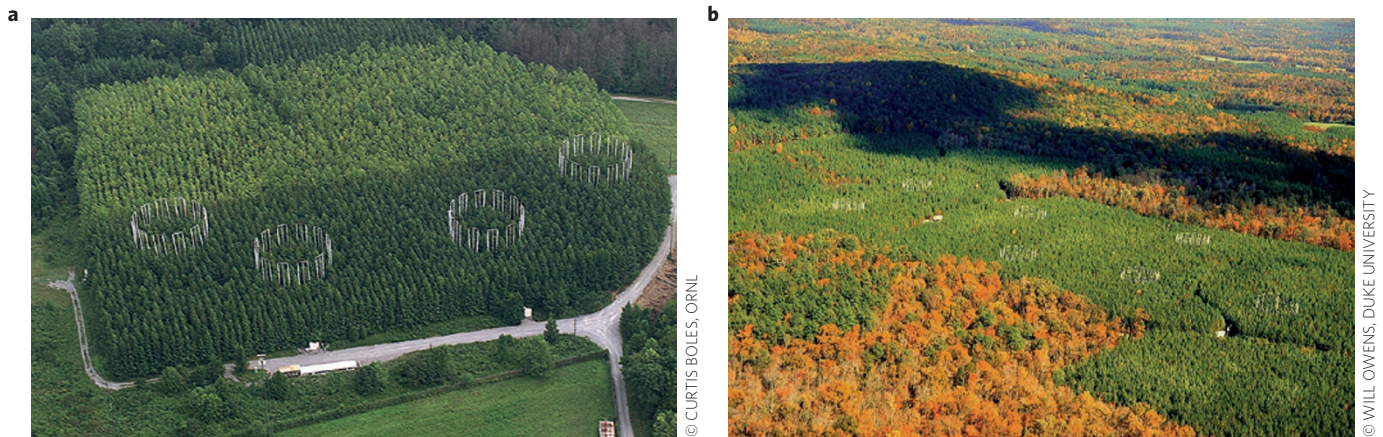


Figure 1 | Aerial views of FACE experiments. a, ORNL FACE experiment; **b**, Duke FACE experiment.

of observed system characteristics, and then ranked according to how well they replicated the observed patterns. While this approach can identify a ‘best’ model for a given data set (or suite of data sets), it rarely leads to model improvement because it does not identify the reasons for good or bad model performance. It also overlooks the problems of equifinality and parameter tuning, which can lead to models performing well for the wrong reasons³⁹.

In contrast, the assumption-centred approach used in the FACE-MDS explicitly aims to identify and evaluate the assumptions causing intermodel differences (Fig. 2b). This approach makes use of the fact that ecosystem models at their core have a similar structure⁴⁰. Each of the models participating in FACE-MDS represents the major processes driving C, water and N fluxes among tree and soil components. The differences among the models thus stem from the specific hypotheses and parameter values used to represent each individual process. As a consequence, the hypotheses representing individual processes can be directly compared among models, and their responses to eC_a assessed.

The basis of the assumption-centred approach is that, instead of investigating the emergent ecosystem-level response, one subset of processes is examined at a time. We used two key analysis tools to do this (Box 1). One tool is model simplification: for a given process, we identify the simplest possible representation for that process and compare it against output from each model. We then ask, what assumptions are made in that model to explain its divergence from the simplest possible representation? A second tool is process decomposition: we mathematically decompose composite variables into component variables that each represents a sub-process of the target process. These types of analyses provide major insights into model behaviour by allowing us to identify the key assumptions that are responsible for differences among model predictions.

The modelled process responses can then be compared against relevant experimental data to identify which of the assumptions are supported by the observations and which are not. In the FACE-MDS we were sometimes, but not always, able to identify the assumption corresponding best to the available observations. In some cases, the FACE experimental data were not sufficient to discriminate among assumptions, indicating a need for additional observations, including non-FACE data. In other cases, it was clear that none of the models were correctly capturing the experimental responses, demonstrating a need for development of new theory. These results are summarized in Fig. 3.

Discrimination among alternative model assumptions

For the following processes (shown in green in Fig. 3), it was possible to distinguish model assumptions that best captured the

experimental responses, leading to clear recommendations for the types of models to use.

Stomatal conductance. There is a relationship between stomatal and photosynthetic responses to C_a , with the strongest reductions in stomatal conductance occurring when photosynthetic increases are smallest and vice versa⁴¹. Models thus commonly represent stomatal responses to C_a as a function of assimilation. The most widely used stomatal conductance models assume that the ratio of assimilation to stomatal conductance is proportional to C_a , but some variants of these models assume a different relationship (see Box 1). Data from the two forest FACE experiments support proportionality, as do a wide range of other experiments^{42,43}, suggesting that the most widely used models are appropriate²⁹.

Allocation. Allocation describes the distribution of NPP among the different plant organs (leaves, wood and fine roots). Of the allocation assumptions considered, we found that ‘functional relationship’ allocation models, in which allocation is calculated to give allometric relationships among plant tissues that vary with resource availability, were best able to capture the general features of the observations. Some models assumed that the fractions of NPP allocated to each tissue were constant, but allocation in the FACE experiments responded dynamically to eC_a , with significantly greater root allocation at ORNL⁴⁴ and slightly greater wood allocation at Duke^{26,30}, so the ‘constant coefficient’ models did not perform well. Similarly, models that used allocation coefficients that were unconstrained by relationships among plant biomass components gave results that were inconsistent with data. We thus recommend allocation models that include dynamic allometric constraints³⁰. Such models may include empirical, optimization or competitive approaches⁴⁵.

N limitation. The ecosystem models differed in how quickly N availability declined owing to eC_a such that it limited plant production. In two models, N limitation was assumed to effectively preclude any stimulation of productivity even at the start of the experiments. This assumption is not supported by either experiment, as site-average productivity was strongly stimulated in the first years at both sites. Limitation of the eC_a effect by N availability occurred at the ORNL site as a gradual process in subsequent years²⁷. These results clearly indicate that models need to allow for a degree of flexibility in the coupling of the C and N cycles²⁸.

Missing or wrong model assumptions

There were a number of processes (shown in red in Fig. 3) for which it was found that no model correctly captured the behaviour

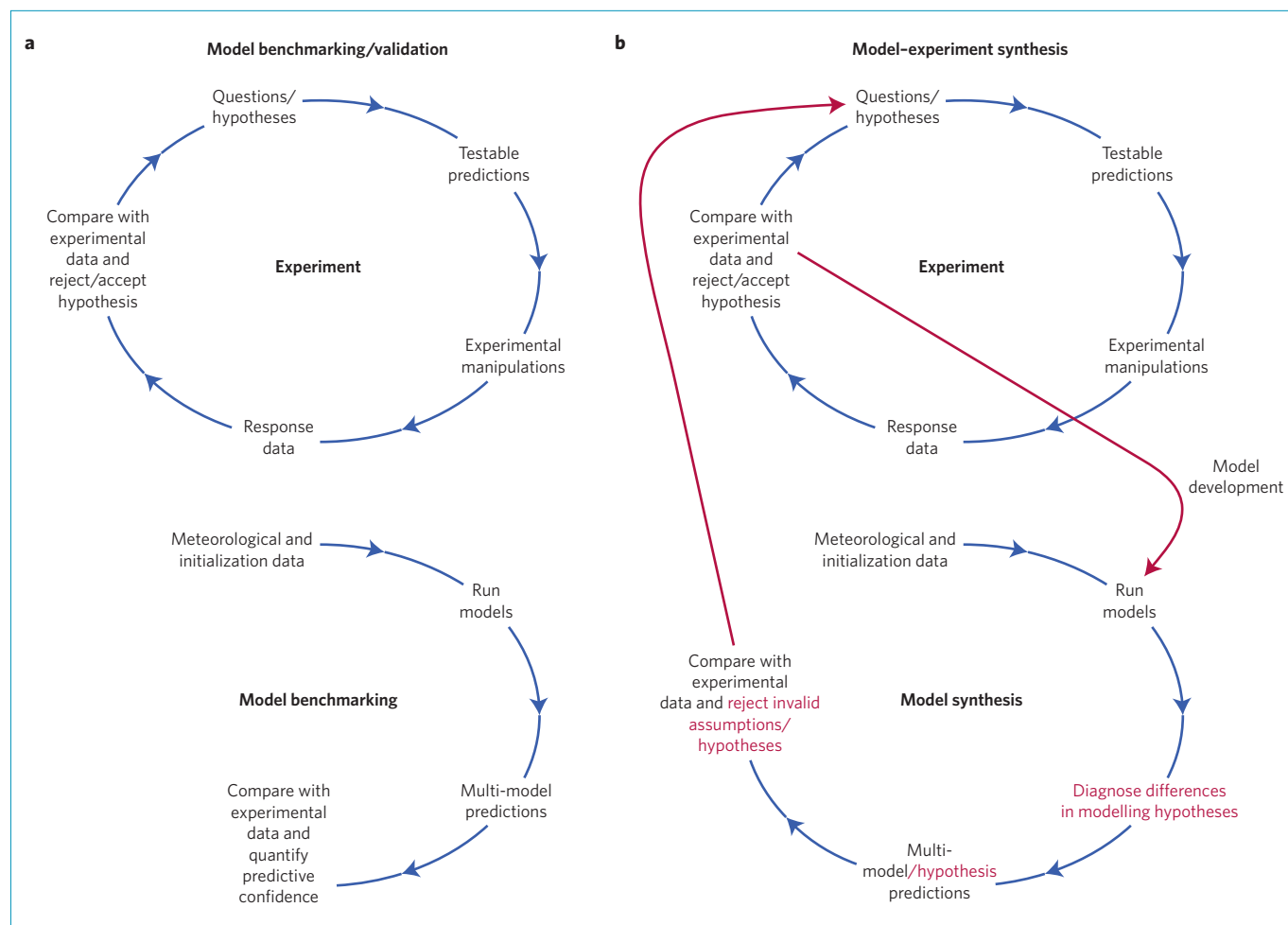


Figure 2 | Comparison of the benchmarking and model-data synthesis approaches to model intercomparison. **a**, Model benchmarking/validation; **b**, Model-experiment synthesis. The assumption-centred approach translates model evaluation into hypothesis testing, allowing a two-way flow of information between modelling and experiment to improve our predictive understanding of the system. Figure adapted with permission from ref. 14, AGU.

seen in the experiments. These cases indicate areas where new theory is needed.

Leaf mass per area. Leaf mass per area (LMA) is important in determining LAI, a key ecosystem property. The experimental data showed an increase in LMA in eC_a , particularly at the single-species, more homogeneous ORNL FACE, which meant that LAI did not respond as strongly to eC_a as did foliage biomass. An increase in LMA is a common observation in eC_a experiments (for example, ref. 9) but was not captured by any of the models; in fact, most of the models treat LMA as a constant. Further theory is needed to predict such changes in LMA and avoid over-prediction of eC_a effects on LAI³¹.

Flexibility of plant stoichiometry. Increasing tissue C/N ratios is one mechanism by which plants can maintain high productivity under nutrient limitation. The experimental data showed a consistent decline of the mass-based foliar N concentration with eC_a . A subset of the ecosystem models under investigation included this acclimation process, which qualitatively increased the agreement with observations. However, all of these models overestimated the extent of stoichiometric acclimation, suggesting that the current models lack an appropriate representation of the fundamental trade-offs governing foliar N allocation²⁸. Theories on foliar N demand are in

development (for example, ref. 46) and may help to determine foliar N demand beyond simple stoichiometric coefficients.

Priming of soil N release. The models underestimated the observation-based net transfer of N from soil organic matter to vegetation associated with eC_a , and thus suggested stronger than observed N limitation at the Duke site, where this net N transfer was substantial. This model failure is very probably owing to a missing representation of the increase in soil organic matter turnover with increased plant rhizodeposition^{47,48}. Such an increase was observed at both sites^{48,49}. However, the magnitude of this effect differed strongly between the sites, alleviating N limitation in the Duke evergreen, needle-leaved site, but not the ORNL deciduous, broad-leaved forest. New theory is needed for the models to incorporate this effect (see refs 50, 51). In addition, slow accrual rates and large standard errors in observations of soil matter content made it difficult to quantify the extent of the model failure, suggesting that improving the accuracy of soil organic matter records is pivotal²⁸.

Additional data are needed for discrimination

In several cases (shown in orange in Fig. 3), the reasons for discrepancies among models were not specific to eC_a , but related to model representation of plant ecophysiological function in general. In these cases, broader data sets and data syntheses are needed to constrain the models.

Box 1 | Examples of analyses used in the assumption-centred approach.

Model simplification. One technique is to compare all outputs for a given process against those from a 'lowest common denominator' simple model. For example, 10 of the 11 models considered here applied similar representations of stomatal conductance. All used different versions of the stomatal conductance model of Ball, Woodrow and Berry⁶⁴. The simplest possible application of this model predicts that WUE, defined as canopy assimilation divided by transpiration, should be proportional to the C_a , independent of model parameterization. We therefore compared modelled WUE against this simple prediction. In two of the models, the difference from the simple model could be attributed to the fact that they used structurally different variants of the Ball, Woodrow and Berry model, which do not yield the same proportional response to C_a . Leaf-level gas exchange data from both experiments supported the simplest possible model rather than the variants²⁹. Thus, this approach allowed us not only to identify an important difference among the assumptions of the models and outline their

importance for predicting the ecosystem-level consequence of CO_2 fertilization, but also to identify which of these assumptions were supported by observations.

Model decomposition. A second technique is to decompose a process into its components to identify which of several underlying assumptions is causing intermodel differences^{28,65}. For example, ref. 28 decomposed net primary production (NPP, $gC\ m^{-2}\ yr^{-1}$) into N use efficiency (NUE, gC per gN) and N uptake (N_{up} , $gN\ m^{-2}\ yr^{-1}$):

$$NPP = NUE \times N_{up}$$

Using this decomposition, ref. 28 showed that, although several models correctly estimated the eC_a effect on NPP, they did so for the wrong reason: effects of eC_a on NUE were overestimated, whereas effects on N_{up} were underestimated.

The relative importance of electron transport and Rubisco limitations to photosynthesis. Most models employ the Farquhar–von Caemmerer model of photosynthesis⁵², in which photosynthesis is determined by the most limiting of two processes, electron transport and Rubisco activity. As Rubisco-limited photosynthesis responds more strongly to changes in C_a than electron-transport-limited photosynthesis, models in which the Rubisco limitation predominates predict larger direct responses of canopy photosynthesis to eC_a ²⁸. Direct empirical tests of theoretical predictions for how the ratio of the two limitations varies on the leaf scale (for example, ref. 53) and on the canopy scale (for example, ref. 54) could help identify the best way to parameterize these processes and thereby reduce intermodel differences.

Sensitivity of transpiration to stomatal conductance. An important cause of differences in the predicted eC_a effect on WUE among models was that the sensitivity of canopy transpiration to stomatal conductance varied dramatically among the models. Although most models predicted that the stomatal conductance would be reduced significantly with eC_a (see 'Stomatal conductance' section), the resultant change in transpiration varied from close to proportional to the change in stomatal conductance, to almost none. Given that there has been much previous work on the strength of coupling of transpiration to canopy conductance (for example, refs 55–57), this discrepancy seems remarkable, and should be resolvable from existing data on canopy coupling²⁹.

Interception. Models disagreed on what fraction of rainfall was intercepted (and evaporated) by the canopy, and how canopy gas exchange was affected when the canopy is wet. Both components noticeably affected the overall water-budget response to eC_a , as eC_a affected the foliar projected cover. A model-oriented review of data on wet canopy function would help to reduce uncertainty around the representation of this component of the water balance²⁹. This issue is particularly important for moist canopies with high leaf area index, such as tropical rainforests.

Drought. Models disagreed on whether low soil-moisture availability affected the ratio of stomatal conductance to photosynthesis, or the biochemistry of photosynthesis, or both²⁹. This assumption strongly affects the WUE response to eC_a under low soil-moisture availability. Evidence emerging from other studies of drought impacts on gas exchange indicates that both processes are impacted by drought^{58,59}, suggesting that models should include both effects.

Turnover. The effect of eC_a on biomass accumulation is strongly affected by the rate at which plant organs, particularly wood, turn over. Most models represented this process with a relatively simple parameterization, and the parameter values chosen differed strongly among models, indicating large uncertainty about this process³⁰. However, the timescale of the FACE experiments (10 years) is clearly too short to constrain this long-term process. Data to constrain this aspect of the models need to come from observational studies rather than manipulative experiments (for example, refs 60, 61).

Ecosystem N losses. The models disagreed strongly on the magnitude of the eC_a effect on ecosystem losses of mineral N through leaching. On the ten-year time scale of this experiment, this disagreement had only a small effect on plant N uptake, because changes in soil organic N turnover had a stronger effect²⁸. However, as changes in ecosystem N losses accumulate over time, for longer-term simulations we will need better-constrained estimates of these losses.

Outcomes

Our new 'assumption-centred' approach to model–data inter-comparison used in the FACE-MDS proved highly successful in several ways. The principal outcome is the clear roadmap, outlined above, for improving model capacity to predict eC_a effects on forests. This roadmap highlights key research tasks for both modellers and experimentalists.

A second major outcome was that our approach provided a strict test of model consistency. Each model was required to output information on C, water and nutrient budgets that allowed us to verify that all models conserved mass and energy, and that fluxes were defined consistently across models. This verification, and the detailed model analysis using the tools outlined in Box 1, identified several cases in which model assumptions had either not been correctly implemented or had unintended consequences³¹. We recommend that modellers apply the assumption-centred analysis tools both in model comparisons and individual model runs as a way of verifying model results.

Third, the FACE-MDS has provided real insights into how and why models differ in their predictions of ecosystem responses to rising C_a . These insights are not limited to the models considered in FACE-MDS. Having highlighted the key alternative assumptions causing intermodel differences, we can classify other models according to which of those alternatives they use, and

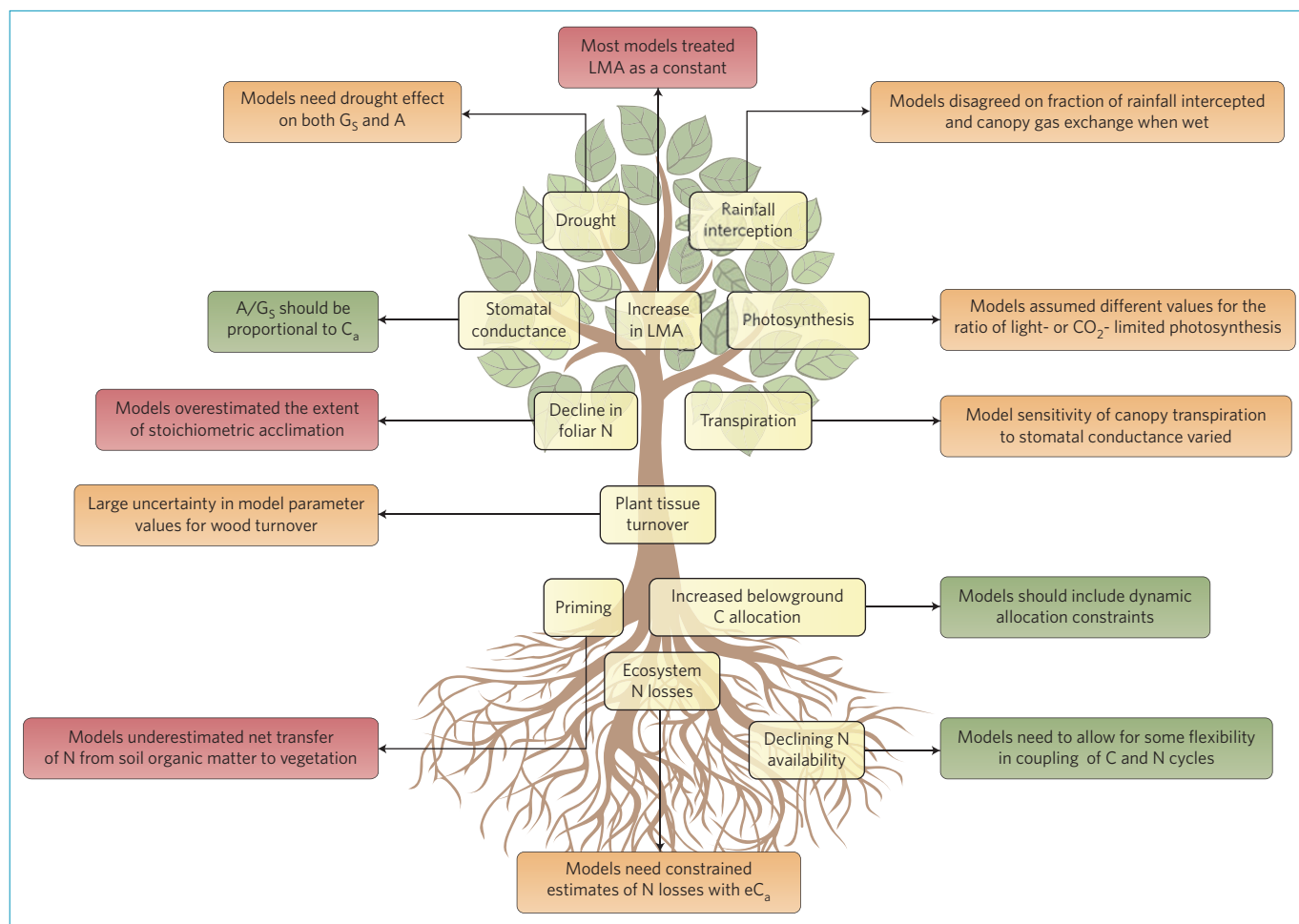


Figure 3 | Visual summary of findings of FACE-MDS project. Green: processes where FACE data sets allowed discrimination among alternative model assumptions; red: processes where FACE data sets identified missing or wrong model assumptions; orange: processes where additional data are needed to discriminate among model assumptions. A, assimilation; G_s, stomatal conductance. Tree diagram © nikitina/olga/iStock/Thinkstock.

interpret their outcomes accordingly. For example, inspection of the assumptions of the JULES model⁶² indicates that transpiration should be strongly coupled to stomatal conductance, implying that this model should give larger responses of WUE to eC_a than models with weaker coupling, such as the LPJ family of models⁶³.

Our approach to model intercomparison could be usefully applied in other, similar projects aiming at synthesizing the outcomes of data-rich ecosystem manipulation experiments into process-based ecosystem modelling. We particularly encourage new experiments to adopt and plan for such a modelling framework as the experiment is established. Early preparation will increase the efficiency with which experimental data are collected and organized for use in models, and a priori modelling allows for the generation of testable hypotheses to guide experimental measurements.

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Competing financial interests

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