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Authors
Harrison, Sandy P
Cramer, Wolfgang
Franklin, Oskar
et al.

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Eco-evolutionary optimality as a means to improve vegetation and land-surface models

Sandy P. Harrison[1,2], Wolfgang Cramer[3], Oskar Franklin[4,5], Iain Colin Prentice[2,6,7], Han Wang[2], Åke Brännström[8], Hugo de Boer[9], Ulf Dieckmann[4,10], Jaideep Joshi[4], Trevor F. Keenan[11,12], Aliénor Lavergne[13], Stefano Manzoni[14], Giulia Mengoli[6], Catherine Morfopoulos[6], Josep Peñuelas[15,16], Karin T. Rebel[9], Youngryel Ryu[17], Nicholas G. Smith[18], Benjamin D. Stocker[19,20], Ian J. Wright[7]

1: Department of Geography and Environmental Science, University of Reading, Reading, RG6 6AB, UK
2: Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth System Science, Tsinghua University, Beijing 100084, China
3: Institut Méditerranéen de Biodiversité et d'Ecologie Marine et Continentale, Aix Marseille Université, CNRS, IRD, Avignon Université, Technopôle Arbois-Méditerranée, F-13545 Aix-en-Provence cedex 04, France
4: International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria
5: Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden
6: Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK
7: Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia
8: Department of Mathematics and Mathematical Statistics, Umeå University, 901 87 Umeå, Sweden
9: Copernicus Institute of Sustainable Development, Environmental Sciences, Faculty of Geosciences, Utrecht University, Vening Meinesz building, Princetonlaan 8a, 3584 CB Utrecht, The Netherlands
10: Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies (Sokendai), Hayama, Kanagawa 240-0193, Japan
11: Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, CA 94720, USA
12: Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, CA, USA
13: Department of Physics, Imperial College London, South Kensington Campus, London SW7 2AZ, UK
14: Department of Physical Geography and Bolin Centre for Climate Research, Stockholm University, SE-106 91, Stockholm, Sweden
15: CSIC, Global Ecology CREAF-CSIC-UAB, Bellaterra, 08193 Barcelona, Catalonia, Spain
16: CREAF, Cerdanyola del Valles, 08193 Barcelona, Catalonia, Spain
17: Departmet of Landscape Architecture and Rural Systems Engineering, Seoul National University, Seoul 08826, South Korea
18: Department of Biological Sciences, Texas Tech University, 2901 Main Street, Lubbock, TX 79409, USA
19: Department of Environmental System Science, ETH, Universitätstrasse 2, CH-8092 Zürich, Switzerland
20: Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

Corresponding author: Sandy P. Harrison (s.p.harrison@reading.ac.uk; +44 1392 851329)

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Summary

Global vegetation and land-surface models embody interdisciplinary scientific understanding of the behaviour of plants and ecosystems, and have become indispensable to project the impacts of environmental change on vegetation and the interaction between vegetation and climate. However, systematic errors and persistently large differences among carbon and water cycle projections by different models highlight the limitations of current process formulations and point to more fundamental problems in how models are developed. In this review, focusing on core plant functions in the terrestrial carbon and water cycles, we show how testable unifying hypotheses derived from eco-evolutionary optimality principles can provide novel, parameter-sparse representations of plant and vegetation processes. New, independently tested modules could profitably be integrated into modelling frameworks that account for the multiple time scales on which plants and plant communities adjust to environmental change.

Key words: eco-evolutionary optimality, global vegetation model, land-surface model, water and carbon trade-offs, stomatal behaviour, leaf economics spectrum, acclimation, plant functional ecology

I. Introduction

The ability of land ecosystems to deliver societal benefits – including the regulation of climate, the carbon cycle and water and air quality, and the provisioning of goods including food and fibre – is at risk because of current rates of global environmental change (Ostberg et al., 2018). Assessing and mitigating this risk requires the reliable characterization of vegetation processes, including plant demography, growth and competition as well as physical land-atmosphere interactions, at multiple spatial and temporal scales. Highly developed, process-based computational models now exist that operate across scales, simulating photosynthesis and stomatal regulation, carbon allocation, competition for light, water and nutrients, community assembly, disturbance regimes, interactions of vegetation with climate and atmospheric composition, and yields of essential products including crops. The two main (overlapping) categories of current models are dynamic global vegetation models (DGVMs) and land surface models (LSMs). LSMs are designed for embedding in climate models and represent "fast" land-atmosphere exchanges explicitly, typically with half-hourly time-steps. Some LSMs treat vegetation composition and structure as static; others simulate vegetation dynamics as well and are therefore also DGVMs. On the other hand, some "offline" (i.e. not coupled to a climate model) DGVMs represent fast land-atmosphere exchanges implicitly, using daily time-steps. Earth System Models (ESMs) are climate models that use LSMs to represent the interactions of the land and ocean surfaces with the state and composition of the atmosphere. LSMs – with or without dynamic vegetation – provide the means for ESMs to represent the land-atmosphere interface, including impacts of atmospheric CO_2 and climate change on vegetation and feedbacks from vegetation changes on CO_2 and climate.

DGVMs and LSMs are based on explicit formulations of a set of processes, rather than on emergent empirical relationships (in contrast, for example, with forest yield tables) and they are generic in terms of plant types considered (in contrast, for example, with most crop models). Process-based vegetation models have been extensively applied by the climate, integrated assessment and impacts modelling communities to assess the nature and impacts of projected climate change, including the role of biophysical and biogeochemical feedbacks. For example, an ensemble of global vegetation models is included in the Global Carbon Project's annual update on the state of the carbon cycle (Friedlingstein et al., 2020), and is widely used to assess the role of vegetation in land-atmosphere interactions, such as diagnosing causes of fluctuations in the atmospheric CO_2 growth rate (Keenan et al., 2016). Vegetation models in general have a wide variety of uses, from quantifying the magnitude of the positive climate-carbon cycle feedback and the negative CO_2 fertilization feedback to climate (e.g. Cox et al., 2013), to investigating the impact of recent climate change on the hydrological cycle (e.g. Ukkola and Prentice, 2013), and projecting the impact of future climate change on crop production (Inter-Sectoral Impact Model Intercomparison Project, ISIMIP2b: https://www.isimip.org/protocol/#isimip2b/; Ostberg et al., 2018).

Modelling vegetation as a fully embedded component of the climate system presents major scientific and computational challenges (Fisher and Koven, 2020). The many successful applications of vegetation models have drawn attention away from several known systematic failures, which have emerged especially when models were used to reproduce large-scale phenomena encoded in atmospheric measurements. For example, both ESMs and offline DGVMs failed to reproduce the full magnitude of the amplification of the high-latitude seasonal cycle of atmospheric CO_2 over the past half-century (Graven et al., 2013; Thomas et al., 2016). DGVMs also failed to reproduce the observed relationship between atmospheric $^{13}CO_2$ content and global land-atmosphere carbon exchange (Peters et al., 2018). Models disagree even about the sign of the effect of global warming on primary production (Ciais et al., 2013). There are large uncertainties in the modelled response of vegetation to precipitation changes (Huntzinger et al., 2017) and little agreement in the simulated response to CO_2 and the role of nutrient availability in modulating this response (Wieder et al., 2015). Large differences in the modelled behaviour of global vegetation, which have persisted for more than two decades (VEMAP 1995; Friedlingstein et al. 2006), were identified as a serious concern in the IPCC Fifth Assessment Report (Ciais et al., 2013). Developments since then have not alleviated this concern (Arora et al., 2020).

These problems suggest a need to re-assess the assumptions and processes included in current vegetation models, and the modalities by which they are developed. The explosion over the last 20 years in the amount and variety of data available – including plant trait databases, field campaigns, flux measurements, ecosystem experiments and satellite remote sensing – should greatly facilitate the process of developing better models. Indeed, meta-analyses of different types of observation have provided insights into universal patterns which can be used for testing general patterns in simulated ecosystem responses to various drivers (Wieder et al., 2019). Finding ways to test alternative hypotheses using observations will also require moving beyond meta-analysis. Large-scale field experiments provide under-utilized opportunities for model evaluation (Medlyn et al., 2015), while controlled-environment experiments are irreplaceable for testing general hypotheses about plant function. Controlled-environment experiments could, for example, help to resolve current disagreements about the impact of changes in CO_2 or nutrients on photosynthetic traits.

Progress, however, also requires coherent, well-motivated hypotheses to test. Franklin et al. (2020) highlighted recent developments that hold promise for improving vegetation models by generating such hypotheses. The concept of eco-evolutionary optimality (EEO) is one of these developments.

EEO invokes the power of natural selection to eliminate uncompetitive trait combinations, and thereby shapes predictable, general patterns in vegetation structure and composition. The term 'eco-evolutionary' expresses the fact that organisms adjust to their environment on both shorter (ecological) timescales and longer (evolutionary) timescales. EEO hypotheses are based on identifying trade-offs that organisms are required to make, for example in land plants between CO_2 uptake and water loss, and expressing these mathematically. At the core of modelling EEO are therefore the mechanistic links between plant functional traits, their implications for resource demand and acquisition and biogeochemical cycling, and their effect on the plant's competitiveness. Mechanistic ecosystem models (LSMs, DGVMs, ESMs) are suited to resolve these links and thus provide a useful framework for investigating how EEO shapes global vegetation function and climate-land feedbacks in the Earth system. (EEO approaches are distinct from parameter optimization methods, which are widely used in the context of existing models.) EEO hypotheses have shown a notable ability to predict observed patterns, providing parsimonious explanations of observations at the leaf (e.g. Smith et al., 2019; H. Wang et al., 2020), plant (e.g. Farrior et al., 2013; Lavergne et al., 2020a) and vegetation (e.g. Franklin et al., 2014; Baskaran et al., 2017) levels. However, there is no recipe to generate a "correct" EEO criterion. EEO formulations have to be assessed against data, like hypotheses in all fields of science.

Many modelling groups are exploring the use of EEO hypotheses to improve the representation of specific processes in vegetation models (e.g. Bonan et al., 2014; De Kauwe et al., 2015; Lin et al., 2015; Ali et al., 2016; Xia et al., 2017; Lawrence et al., 2019). In this review, we aim to raise awareness of the broader potential for a hypothesis-testing approach based on EEO to underpin a more far-reaching improvement in the robustness and reliability (*sensu* Prentice et al., 2015) of vegetation models. Section II provides a perspective on the shortcomings of current models and model development practice, informed by our collective experience. Section III introduces case studies that exemplify how EEO can improve (and often, simplify) formulations of core processes at the leaf level that are required by both LSMs and DGVMs. Section IV considers the scope for applying EEO at the whole-plant and plant community levels. Section V deals with limitations of the EEO concept. Section VI briefly considers the outlook for next-generation vegetation models incorporating EEO principles.

II. Model development: problems and solutions

The origins and historical development of global vegetation models have been reviewed by Prentice et al. (2007), Quillet et al. (2010), Prentice & Cowling (2013) and Fisher et al. (2014); this material will not be revisited here. Current models have much in common. Processes are differentiated by operational time-steps: canopy-atmosphere energy exchanges and photosynthesis are modelled in LSMs typically at half-hourly time-steps; phenology, carbon allocation and growth at time-steps of days to months; and vegetation dynamics and disturbance in DGVMs at time-steps of months to years. The diversity of plants is still treated in many models as a limited set of PFTs, each characterized by a distinct set of attributes. However, an important trend over the past decade has been towards the replacement of PFTs by quantitatively varying functional traits. It is now widely recognized that the assignment of fixed sets of traits per PFT is too restrictive, because (a) for most quantitative plant traits, variation is greater within than between PFTs (Kattge et al., 2020), and (b) a substantial fraction of the observed variation in community-mean trait values along environmental gradients is linked to acclimation and adaptation within species and PFTs (Siefert et al., 2015). Progress is being made towards replacing fixed PFTs in models with quantitative traits that vary dynamically, mimicking acclimation and/or adaptation processes (van Bodegom et al., 2012) and more realistically portraying ecosystem carbon uptake (Verheijen et al., 2015) and the dynamic response of terrestrial ecosystems to climate change (Sakschewski et al., 2015).

A number of problems (see Box) however are slowing progress. Some of these may have arisen because of the general institutional separation of model development from empirical science, and the accretional nature of much of this development. Some are practical issues about the way model codes are written, updated and tested. All could be mitigated by adopting different practices (see Box). Several initiatives have promoted systematic data-model comparison ("benchmarking") of land models as a partial remedy for these problems (https://www.ilamb.org/; Collier et al., 2018). Some proposed benchmark data sets – e.g. for upscaled gross primary production (Tramontana et al., 2016) and plant litter properties (Pettinari and Chuvieco, 2016) – however are themselves modelled outputs, which limits their usefulness. Wieder et al. (2019) drew attention to the limitations of benchmarking, which (we suggest) should be considered as a necessary but by no means sufficient part of model evaluation. Wieder et al. (2019) described the recent history of a leading LSM, the Community Land Model (CLM), in particular its evolution from version 4 (a pioneering attempt to include the coupling of ecosystem carbon and nitrogen cycles, which however greatly underestimated global land carbon uptake and its sensitivity to climate) to the better-performing version 5. They made a strong case for the need to use observational and experimental information as an integral part of model development and improvement. Although experimental and observational studies in this field are often justified by the need to improve vegetation models, the pathway by which this new knowledge is transferred is indirect at best. In principle, experiments could be performed precisely to clarify how individual processes should be represented in models. This is still far from being standard practice.

A further consequence of the current model development paradigm is the 'complexity trap' (Franklin et al. 2020). Many recently published model "improvements" are achieved by adding complexity (Fisher and Koven, 2020), but it is generally understood that this does not equate to increased realism – particularly as the incorporation of new processes often increases further the number of poorly known parameters that need to be specified. Moreover, developing models by accretion has inevitably led to a decline in transparency (Prentice et al., 2015). In other areas of environmental modelling, including climate modelling, there has been a growing realization that re-examination of basic processes, reduction of complexity, and increased transparency are all necessary for progress (Held, 2005; Gramelsberger et al., 2020). Vegetation modelling is no exception.

Different Earth subsystems however pose specific challenges. The key challenge for global-scale modelling of biological systems is to identify principles applicable across diverse and phylogenetically distinct assemblages (Franklin et al., 2020). EEO has a key role to play because it can generate coherent, testable hypotheses about plant and vegetation function that transcend differences among biomes and floras. In the following section, we summarize a number of case studies that demonstrate this capability, where EEO approaches have provided parsimonious representations of core, leaf-level processes that are individually testable and supported by evidence. Such representations are candidates to replace the (often more complex and less well-tested) formulations currently in use; however, much research remains to be done to establish the most effective representation for each process. Case studies are presented roughly in descending order of readiness – from photosynthesis and primary production, where a proof-of-concept for implementation in a LSM framework exists, to the leaf economics spectrum, which requires a novel approach to account for how phylogeny and environment co-determine plant traits.

III. Leaf-level optimality

Photosynthesis and primary production. Nearly all LSMs and DGVMs simulate photosynthesis using the FvCB model (Farquhar et al., 1980) or the modification proposed by Collatz et al. (1991). Implementing the FvCB model requires three parameters: the maximum carboxylation rate (V_{cmax}), which determines the enzymatic capacity for carbon fixation; the maximum electron-transport rate (J_{max}), which determines the capacity to generate the required reducing power; and the ratio of leaf-internal to ambient CO_2 (c_i:c_a, here denoted as χ), which relates the assimilation rate to stomatal conductance. Improved understanding of how V_{cmax} and J_{max} vary with environmental conditions should provide a more rigorous basis for modelling photosynthesis and primary production (Rogers et al., 2017). Light use efficiency (LUE) models – widely used in remote-sensing applications – simulate primary production using empirical response functions; this can limit the number of parameters to be estimated but severs the link to processes. These two approaches can be reconciled by applying two EEO hypotheses: the "least-cost hypothesis" that the combined costs of maintaining water loss and carbon uptake pathways are minimized, allowing prediction of stomatal behaviour (Dewar et al., 2018); and the "coordination hypothesis" that V_{cmax} and J_{max} acclimate to growth conditions, so that the capacity of the leaf to fix carbon remains close to the level required to use the available light (Field and Mooney, 1986; Chen et al., 1993; Maire et al., 2012; Quebbeman and Ramirez, 2016; H. Wang et al., 2017). The result is a model applicable to all C_3 plants that has the convenient mathematical form of a LUE model (H. Wang et al., 2017). It has only two new parameters, both of which can be estimated from independent data sets. It yields good agreement with gross primary production (GPP) data derived from eddy-covariance flux measurements (Stocker et al., 2020). It also predicts a number of related physiological characteristics correctly, including the global pattern of V_{cmax} in relation to light, temperature and vapour pressure deficit (VPD) (Smith et al., 2019), elevational trends in photosynthetic traits and primary production (Peng et al., 2020), and the response of V_{cmax} to atmospheric CO_2. Specifically, the model predicts a decline in V_{cmax} with increasing ambient CO_2 (H. Wang et al., 2017), and a steeper increase with decreasing ambient CO_2. Both have been verified experimentally (Figure 1).

Neglecting the adaptive adjustment of V_{cmax} to growth conditions could result in simulated PFTs becoming (unrealistically) maladapted to environmental changes, and (if set too low) unrealistically steep responses of photosynthesis to temperature and ambient CO_2. The model for GPP outlined above (H. Wang et al., 2017) provides an example of how EEO hypothesis formulation and testing can lead not only to a more realistic representation of a key process, in the sense of being well supported by observational and experimental data, but also to a less complex one. Compared to conventional models, the number of parameters required as input has been dramatically reduced, by two mechanisms. First, the adaptive adjustment of key quantities (V_{cmax}, J_{max}, and a variable ξ that determines the response of χ to VPD) eliminates the need for these to be prescribed. Second, it removes the need to provide lists of parameter values for PFTs.

The model is not suitable for immediate incorporation into a LSM because it works on multi-day timesteps (i.e. at the time scale of leaf- and canopy-level acclimation). However, the fast responses of photosynthesis and stomatal conductance to environmental variations are already well characterized (Farquhar et al., 1980; Medlyn et al., 2011). All that is needed, then, is to replace fixed values of V_{cmax} and J_{max} at 25˚C (V_{cmax25}, J_{max25}) and ξ with slowly time-varying values that follow the EEO criteria. This is straightforward in principle, and allows the same model to reproduce measured daily cycles of GPP in different biomes with unchanged parameter values (Figure 2; Mengoli et al., submitted). Moroever, whereas adding a new process (acclimation of photosynthetic parameters) might be expected to increase model complexity, this example shows the opposite: treating acclimation as an EEO process allows GPP to be represented more parsimoniously than would otherwise have been possible.

Dark respiration. Leaf mitochondrial respiration supports many metabolic processes, including the protein turnover required to maintain photosynthetic capacity. Leaf dark respiration (R_{dark}) is a widely measured quantity. Its instantaneous temperature response is commonly represented by the Arrhenius equation (Atkin et al., 2017). Many models assume that R_{dark} at 25°C (R_{dark25}) is proportional to V_{cmax25}, treat this as a constant per PFT, and model the temperature-dependence of both R_{dark} and V_{cmax} with Arrhenius equations. However, there is considerable spatial and temporal variability in R_{dark} within PFTs as a function of environmental conditions (Atkin et al., 2015; Smith and Dukes, 2018). In a global analysis, H. Wang et al. (2020) showed that values of R_{dark} at current growth temperature are optimized according to the need to ensure that its metabolic functions are coordinated with V_{cmax}. This hypothesis predicts that acclimated values of both R_{dark} and V_{cmax} increase with growth temperature – but less steeply than their instantaneous responses to temperature, which are fully compensated by acclimation. These predictions are well supported by data; the conventional modelling approach is not (Figure 3).

Neglecting the acclimation of leaf-level respiration is likely a major source of uncertainty in model predictions, with serious consequences for the estimation of land carbon uptake especially in warmer climates (Huntingford et al., 2017). As with photosynthesis, there is no obstacle in principle to including leaf-level respiratory acclimation in DGVM or LSM frameworks. To do so requires only that R_{dark25} vary along with (slowly varying) V_{cmax25} following H. Wang et al.'s (2020) EEO hypothesis, while the fast environmental responses of R_{dark} and V_{cmax} are represented as in current models (or better, for R_{dark}, via the universal temperature response reported by Heskel et al., 2016). Such a scheme has not been implemented yet, as far as we are aware, in any vegetation model.

Stomatal behaviour and transpiration. Plants regulate water and energy exchanges with the atmosphere by adjustment of stomatal conductance (g_s). Most current models represent g_s based on the fast, experimentally observed response to VPD (Damour et al., 2010). More mechanistic models have been developed (e.g. Sperry et al., 2017), but require new parameters (Drake et al., 2017). EEO hypotheses, based on the trade-off between maximizing carbon gain and minimizing water loss, potentially offer parsimonious solutions. One approach (Medlyn et al., 2011) is based on an approximate solution to the 'CF' hypothesis of constant marginal water use efficiency, originally proposed by Cowan and Farquhar (1977). This solution correctly predicts stomatal responses to changing CO_2 and variability across environmental gradients (Medlyn et al., 2011; Medlyn et al., 2013; Lin et al., 2015). It has been included in land-surface models (e.g. De Kauwe et al., 2015; Oliver et al., 2018) and shown to perform as well as the empirical relationships originally used. These approaches all require calibrating one 'free' parameter per PFT in the optimal stomatal conductance formulation. To achieve a parameter-free formulation, it is possible to re-frame the CF hypothesis by accounting for soil moisture dynamics in the optimization problem (Manzoni et al. 2015), but this implies an assumption on how much soil water can be used by plants.

A different approach (Prentice et al., 2014), used in the model of H. Wang et al. (2017), is based on the EEO hypothesis that leaves minimize the sum of the maintenance costs (per unit assimilation) of transpiration and carboxylation. Carboxylation costs are envisaged as the respiration required for Rubisco turnover, while transpiration costs are envisaged as the respiration required to maintain living sapwood. This hypothesis leads to a mathematical formulation of the fast response of stomata to VPD that is similar to that of Medlyn et al. (2011), while also correctly predicting the environmental dependencies of the control parameter (ξ) on temperature (Lin et al., 2015) and atmospheric pressure (Körner and Diemer, 1987). Each of these predicted partial dependencies of χ on environmental variables can be observed in stable carbon isotope ratio ($\delta^{13}C$) measurements on leaves (H. Wang et al., 2017). Lavergne et al. (2020a; Figure 4) showed they are also present in tree-ring $\delta^{13}C$ measurements. By providing time-series, Lavergne et al. (2020a) moreover confirmed the (weak) dependency of χ on atmospheric CO_2 (Figure 4) that is predicted by this EEO hypothesis. Apart from the well-known VPD response, none of these dependencies is reflected in standard LSMs, except crudely, through the assignment of distinct parameter values to PFTs that occupy different climates.

Further alternative EEO approaches (e.g. Wolf et al., 2016; Anderegg et al., 2018; Eller et al., 2018; Venturas et al, 2018; Trugman et al., 2019; Deans et al., 2020; Eller et al., 2020; Sabot et al., 2020) incorporate hydraulic costs, based on the hypothesis that the short-term and long-term costs of transpiration at low soil water potential contribute to the total cost of maintaining the water transport pathway. The Wolf et al. (2016) formulation has been shown to be in good agreement with experimental evidence for changes in stomatal conductance in response to daily and seasonal changes of environmental conditions, and to perform much better than the CF model in predicting stomatal responses to dry soils (Anderegg et al., 2018). Y. Wang et al. (2020) found that among eleven optimality-based stomatal models, the most skilled were those taking into account the cost of stress-induced hydraulic failure.

The development of EEO hypotheses for stomatal behaviour is a highly active research field. The hypothesis of Prentice et al. (2014) provided an equation with good predictive power for the responses of leaf and plant $\delta^{13}C$ to the growth environment, but its single "universal" parameter has been shown to be influenced by soil moisture (Lavergne et al., 2020b) and soil pH (H. Wang et al., 2017; Paillassa et al., 2020). Moreover, the variation of χ on long climatic moisture gradients appears to be significantly steeper than predicted by that equation (Dong et al., 2020). Allowing variation of ξ following the EEO criterion of Prentice et al. (2014) would allow stomatal acclimation to changes in growth temperature (Marchin et al., 2016). This cannot happen in current models, because their responses to VPD are pre-determined by PFT. However, further research is needed to determine how soil influences might best be included in models. Solutions are likely to include EEO approaches to explain the coordination of hydraulic and photosynthetic traits (Brodribb, 2009; Joshi et al., 2020), and the influence of soil water and fertility factors on water and nutrient acquisition costs (Paillassa et al., 2020).

Isoprene emission. Plant emissions of the volatile organic compound (VOC) isoprene protect photosynthetic function against damage due to reactive oxygen species (ROS), which are produced in leaves at high temperatures (Niinemets, 2010; Harrison et al., 2013; Lantz et al., 2019). As a result, tree species that produce isoprene are competitively favoured under hot and dry conditions (Taylor et al., 2018). Modelling of plant VOC emissions is important in ESMs, because these reactive compounds have a significant impact on atmospheric chemistry. Many ESMs rely on a complex empirical model (Guenther et al., 2006) to predict VOC emissions. More explicitly process-based models of VOC emission have been devised (e.g. Pacifico et al., 2011) but still require several, poorly known parameters to be specified.

However, the responses of isoprene emission to light, temperature and CO_2 are consistent with a much simpler relationship: a linear dependency on the leaf's "energetic status", which is the difference between photosynthetic electron transport and the electron requirement to support the current rate of carbon fixation (Morfopoulos et al., 2013). This relationship reproduces the shapes of observed responses of isoprene emission to environment, including its non-linear response to light (Figure 5); its (otherwise enigmatic) decline with instantaneous increases in ambient CO_2 (Morfopoulos et al., 2013, 2014); and its recovery over time at high CO_2 (Sun et al., 2013). Without this recovery, isoprene-emitters under high CO_2 would lose the thermo-protective benefits of isoprene emission – an unlikely outcome in evolutionary terms.

The leaf energetic status model has the potential to simplify the representation of VOC emission in ESMs, while increasing its predictive power for conditions outside those currently observed. However, a key unanswered question remains, regarding the "base rate" of isoprene emission at the plant-community level. The current standard approach relies (unsatisfactorily) on a fixed geographic field of emission capacity. Explicit hypotheses to predict VOC emission capacity remain to be formulated and tested.

Leaf economics. Leaf mass per unit area (LMA) determines how much leaf area can be produced for a given total aboveground carbon allocation (Cui et al., 2019). The leaf economics spectrum (Wright et al., 2004) relates LMA and leaf lifespan (LL) across all PFTs. In nature, this relationship is not fixed, however, and varies with climate. Kikuzawa (1991) hypothesized that LL maximizes leaf carbon gain over the lifetime of the leaf, accounting for (amortized) leaf construction costs. This EEO hypothesis has recently been combined with two others. Xu et al. (2017) provided empirical support for the hypothesis that the leaf ageing rate (a parameter in Kikuzawa's model) is inversely proportional to LMA, and also to V_{cmax25}; while the coordination hypothesis, described above, predicts optimal values of V_{cmax25}. Combining these three hypotheses leads to a theoretical prediction of the leaf economics spectrum, and how it varies across environments. For winter-deciduous woody plants where LL is constrained by the length of the growing season, this theory leads to a prediction of LMA that is consistent with observations along an elevational and aridity gradient (H. Xu et al., 2020). For evergreen plants it leads to a correct global prediction of the proportionality between LMA and LL, and how this is modified by growing-season length and light (Figure 6). A changing climate will inevitably alter the competitive balance among species with different LMA and LL, in ways that fixed-PFT LMA schemes cannot capture.

In addition to affecting leaf lifespan, LMA mechanistically affects stomatal responses (Buckley et al., 2015). Increasing LMA reduces the conductivity of the outside-xylem water pathway due to increased path-length, and therefore causes highly negative water potentials near the stomata. This in turn may necessitate a greater investment in leaf hydraulics in high-LMA species. Without such investment, these species would be uncompetitive due to reduced photosynthesis rates. Thus, EEO suggests a testable linkage between physiological and hydraulic traits.

The EEO basis for the leaf economics spectrum has not been incorporated in any vegetation model, and its consequences for climate-change impacts are largely uncharted. LMA and LL, as structural/morphological traits, differ from the physiological traits discussed above in showing far less plasticity (or genotypic adaptation) along environmental gradients (Dong et al., 2017, 2020). Therefore, their representation in models calls for a different treatment, as any change in community-mean LMA and LL will depend more on species replacement (a slower process) than on physiological adjustment. In addition, whereas the theory summarized above predicts environmentally conditioned changes in the *relationship* between LMA and LL, it does not predict anything about their mean values. Phylogenetic determinism may be helpful here. Starting from the observed global distributions of these traits, it is possible to calculate how these intersect with the predicted LMA-LL relationship. This will however require representing traits in models as probability distributions rather than as single values.

IV. Beyond the leaf level

Applications of EEO concepts in vegetation modelling have mainly focused on leaf-level processes, because of the short timescale of some leaf-level responses to environmental conditions. The EEO framework however extends naturally to the whole-plant level, providing insightful approaches to modelling processes including phenological timing (Caldararu et al., 2014; Manzoni et al., 2015) and strategy, and carbon allocation to leaves, stems and roots (e.g. Valentine and Mäkelä, 2012; Kvakić et al., 2020). We summarize some cases below.

Carbon allocation. Both field and experimental data show that allocation to roots increases when nutrient supply is limiting, for example on infertile soils or in cold climates (Reich et al., 2014; Gill and Finzi, 2016). This observation is consistent with the long-established EEO hypothesis (Rastetter and Shaver, 1992; Thomas and Williams, 2014; Rastetter and Kwiatkowski, 2020) that plants, requiring multiple resources, allocate effort optimally so that no one resource is limiting to growth. A plant-level allocation model based on this assumption has been used to explain the contrasting effects of elevated CO_2 on tree growth and nitrogen uptake and their dependence on soil nitrogen availability (Franklin et al., 2009; Figure 7). An EEO approach to carbon allocation has been adopted in at least one LSM (Xia et al., 2017).

Soil-plant interactions and mycorrhizae. Carbon exchanges between plants and their symbionts can also be described using EEO principles. The effects of nutrient limitation are predictable based on the carbon costs of nitrogen uptake via different symbionts (Terrer et al., 2018), which may in turn depend predictably on soil nutrient availability (Franklin et al., 2014). The fraction of GPP allocated to sustain symbionts thus becomes an outcome, rather than being imposed as an additional parameter (Baskaran et al., 2017). Modelling soil-plant interactions explicitly in terms of the carbon cost of nitrogen acquisition has a significant impact on modelled primary production (Brzostek et al., 2014) and has been adopted in at least one LSM (Shi et al., 2016). Dynamically linking plants and microbes in a terrestrial biosphere model has been shown to improve predicted carbon and nitrogen dynamics across a gradient of vegetation stands varying in the abundance of trees with distinct (arbuscular and ectomycorrhizal) types of mycorrhizal interaction (Sulman et al., 2017).

Demography and species replacement. Community-mean trait values are to some extent an outcome of acclimation by individual plants, but also of adaptation: environmental filtering ensures that genotypes and species are present only in environments that fall within their acclimation capacity.

The extent to which the observed variability in plant functional traits is due to phenotypic plasticity (individual acclimation) or to non-plastic genotypic differentiation and species replacement (Meng et al., 2015; Yang et al, 2018; Dong et al., 2017, 2020) has received little attention in the modelling literature, yet it is essential information for understanding how community function and composition react to rapid environmental changes. Plastic traits, such as photosynthetic capacity (Togashi et al., 2018a) and the temperature optimum of photosynthesis (Kumarathunge et al., 2019; Vico et al., 2019), acclimate quickly (days to weeks) within individual leaves; while other leaf traits, including LMA, show only partial within-species adjustment to changes along environmental gradients (Dong et al., 2017, 2020). Hydraulic traits, particularly leaf hydraulics linked to LMA and wood properties in general, are also expected to show limited plasticity. Adaptive changes in the mean abundance of non-plastic traits can only occur through the slower processes of community dynamics, which depend on demography and competition among species. How best to represent these processes is a highly active field of DGVM research (e.g. Reichstein et al., 2014; Sakschewski et al., 2015: Fisher et al., 2018; Longo et al., 2019; Argles et al., 2020).

Competition and coexistence. There is a potential for optimality-models to represent not only single optimal plant strategies but also coexisting strategies, which determine how resources are partitioned as determined by diversity in plant function. Examples include the coexistence of different strategies for coping with water shortage in dry environments (Lindh et al., 2014), and the complementarity of alternative life-history strategies generating within-site heterogeneity and corresponding variation in optimal strategies in resource-rich communities (Togashi et al., 2018b). Falster et al. (2017) demonstrated the evolution of stable coexistence of tree species in a height-structured competition model related to the demographic schemes used in DGVMs. This work offers the prospect of a wider field of application for EEO-based modelling to address the origins and maintenance of species diversity.

V. Outstanding issues

It should be abundantly clear from the discussions above that EEO, despite its utility, is not a “magic bullet” that can instantly resolve problems in LSM and DGVM development. We suggest instead that EEO concepts should underpin a research programme in which explicit, quantitative hypotheses play a central role in data analysis and experimental design, while also providing parsimonious formulations for modelling. Practitioners of this integrative approach need to be aware of the limitations of EEO as well as its strengths. Some of the most important limitations are summarized below.

Natural selection acts on reproductive fitness, not on plant growth. However, reproductive fitness is practically impossible to measure in plants in the field. EEO hypotheses can be formulated in terms of vegetative properties but it must be recognized that these are only indirectly linked to fitness. The underlying assumption is that ineffective or uncompetitive trait combinations will confer low fitness and be selected against.

It follows from the above that *no EEO hypothesis is unique*. For every trade-off considered, there are alternative criteria all of which might appear to be compatible with EEO, but which make different predictions. (Some examples have been discussed above.) Only empirical tests can determine which, if any, of a series of alternative EEO hypotheses makes realistic predictions.

The limits to optimality are a priori *unknown* and can only be assessed empirically. Recent EEO approaches to photosynthetic optimality illustrate pragmatic choices that have to be made in the interests of parsimony. For example, it has been assumed that certain photosynthetic traits can show unlimited variation, while others – such as the Michaelis constants and specificity of Rubisco, the intrinsic quantum yield of electron transport, and their temperature dependencies – are constants. These assumptions are supported by observations but only as an approximation; all of these properties do in fact vary among plants (Ehleringer and Piercy, 1983; Dreyer et al., 2001; Singsaas et al., 2001; Galmés et al., 2015; Galmés et al., 2016), even if their variation is relatively modest.

Optimality is approached at different rates by different processes. In a realistically time-varying environment optimality is approached rather than achieved, because the optimum is a moving target. We have distinguished the fast (minutes to hours) time scales of enzyme kinetics and stomatal responses to VPD from the slower time scales of leaf-level physiological acclimation (days to months), carbon allocation (months to years) and species replacement (years to decades). DGVMs respect these distinctions. However, the shift from a PFT to a trait basis for modelling necessitates ensuring that trait shifts dependent on species replacement take place on the appropriate time scale, which can be different for different traits. One method to achieve this for non-plastic traits, without enumeration of actual species, is by sampling from a multidimensional trait space (Fyllas et al., 2014).

The problem of absent species. A harder issue related to time scales is how to represent dispersal and migration (in other words, species replacement when the best-adapted species are not locally present) in DGVMs. Attempts to do so are not reviewed here. However, we note that existing approaches will remain speculative unless it can be shown that the rates of migration they predict are consistent with observed rates of species replacement in response to rapid climate changes in the past (e.g. Harrison and Sanchez Goñi, 2010).

The importance of experiments. Comprehensive testing of EEO hypotheses cannot rely entirely on meta-analysis. Data from direct environmental manipulations are not hampered by correlations between environmental variables and can therefore be used to quantify the time-scales of responses (Kumarathunge et al., 2019). Controlled-environment greenhouse experiments have been used to determine the rates and mechanisms underlying acclimation of photosynthetic (e.g. Scafaro et al., 2017), hydraulic (e.g. Locke et al., 2013) and leaf-biochemical parameters (e.g. Dongsansuk et al., 2013) to changes in the growth environment. Field experiments can scale individual to ecosystem-level responses, through direct manipulations (e.g. Hoeppner and Dukes, 2012; Hovenden et al., 2019), exclusion experiments (e.g. Inoue et al., 2017; Tomasella et al., 2018) or opportunistic sampling strategies (e.g. Lusk et al., 2018). The increasing coordination of field experiments, including experiments to examine the impacts of manipulating nutrient (e.g. NutNet; Borer et al., 2013) or water supplies (e.g. DROUGHT-NET: Knapp et al., 2017), provides opportunities to evaluate the role of different plant strategies for coping with environmental stresses, and such networks provide key targets for model evaluation (e.g. Hilton et al., 2019).

Disturbance and land use. Theory regarding natural disturbances in vegetation is rudimentary. Models for the interaction of wildfire regimes with vegetation and climate have been developed, but their performance is relatively poor beyond the largest-scale geographic patterns (Forkel et al., 2019; Hantson et al., 2020), and they struggle to represent the modification of natural processes by land management and human settlement patterns. Even so, there is scope for EEO concepts to inform research and ultimately improve models. For example, plants have evolved specific adaptations to different frequencies and intensities of fire (Clarke et al., 2013; Pausas et al., 2016; Pausas, 2019) which must be represented in vegetation models if they are to project the consequences of environmental changes in fire-prone regions realistically. Simulating the land biosphere under direct human intervention (including agriculture, pastoralism and forestry) presents further challenges. Much research attention has focused on the data required to impose land-use history on vegetation models (e.g. Pongratz et al., 2008; Klein Goldewijk et al., 2017). More could usefully be focused on the function of modified ecosystems. Arable crops represent an extreme modification of the landscape, yet crop growth conforms to the same principles as all plants and can be modelled with the same EEO-based tools (Qiao et al., 2020).

VI. Concluding remarks

Vegetation models have shown their usefulness for projecting ecosystem productivity, vegetation patterns, terrestrial carbon uptake and other ecosystem services in a rapidly changing world. These projections now feed routinely into global assessments such as those being made by the IPCC, the

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Integrated Research on Disaster Risk project. Thus, they contribute to the evidence base necessary to assess progress towards the United Nations Sustainable Development Goals. However, more reliable models are required to enhance confidence in the plausibility of many of these projections. The rates of expected global environmental change increases the need for models to be able to deal with dynamic processes, including plant migration, adaptation, acclimation and land-use change. Global changes are occurring faster than many adaptive processes and are likely to result in novel environmental conditions; models must therefore be equipped to deal with non-equilibrium situations and novel conditions outside the range for which they were originally developed and tested. This can only be achieved by ensuring that they realistically account for acclimation and adaptation processes and do not entirely rely on statistically determined, historical patterns. However, increased realism is of little value if it is accompanied by over-parameterization and ever-increasing parameter uncertainty. We have indicated how EEO theory can provide a means to alleviate these problems. It requires clear formulation of alternative hypotheses, which in turn creates a central role for observations and experiments to test and compare them.

There is as yet no comprehensive description of plant behaviour in terms of EEO – indeed, as some of the examples above have shown, the appropriate choice of optimality criteria is an active research topic in areas such as stomatal behaviour while in other areas, such as disturbance dynamics, EEO concepts are in their infancy. Moreover, there is no recipe for success. EEO hypotheses must be tested, and many will fail. EEO approaches are nonetheless providing robust, parsimonious and well-supported representations of core processes that are represented in all vegetation models, and offer promise for the development of a new generation of models.

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References

Anderegg WRL, Wolf A, Arango-Velez A, Choat B, Chmura DJ, Jansen S, Kolb T, Li S, Meinzer FC, Pita P, Resco de Dios V, Sperry JS, Wolfe BT, Pacala S. 2018. Woody plants optimise stomatal behaviour relative to hydraulic risk. *Ecology Letters* **21**: 968-977, doi:10.1111/ele.12962

Argles APK, Moore JR, Huntingford C, Wiltshire AJ, Jones CD, Cox PM. 2020. Robust Ecosystem Demography (RED version 1.0): a parsimonious approach to modelling vegetation dynamics in Earth system models. *Geoscientific Model Development* **13**: 4067-4089, doi: 10.5194/gmd-13-4067-2020

Arora VK, Katavouta A, Williams RG, Jones CD, Brovkin V, Friedlingstein P, Schwinger J, Bopp L, Boucher O, Cadule P, Chamberlain MA, Christian JR, Delire C, Fisher RA, Hajima T, Ilyina T, Joetzjer E, Kawamiya M, Koven C, Krasting J, Law RM, Lawrence DM, Lenton A, Lindsay K, Pongratz J, Raddatz T, Séférian R, Tachiiri K, Tjiputra JF, Wiltshire A, Wu T, Ziehn T. 2020. Carbon-concentration and carbon-climate feedbacks in CMIP6 models, and their comparison to CMIP5 models. *Biogeosciences* **17**: 4173-4222, https://doi.org/10.5194/bg-2019-473

Atkin OK, Bahar NHA, Bloomfield K, Griffin KL, Heskel MA, Huntingford C, Martinez de la Torre A, Matthew H. Turnbull MH. 2017. Leaf respiration in terrestrial biosphere models. In Tcherkez G, Ghashghaie J (eds), *Plant Respiration: Metabolic Fluxes and Carbon Balance*, Springer International Publishing AG, Switzerland, pp. 107-142.

Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G, Bradford MG, Cernusak LA, Cosio EG, Creek D, Crous KY, Domingues TF, Dukes JS, Egerton JJG, Evans JR, Farquhar GD, Fyllas NM, Gauthier PPG, Gloor E, Gimeno TE, Griffin KL, Guerrieri R, Heskel MA, Huntingford C, Ishida FY, Kattge J, Lambers H, Liddell MJ, Lloyd J, Lusk CH, Martin RE, Maksimov AP, Maximov TC, Malhi Y, Medlyn BE, Meir P, Mercado LM, Mirotchnick N, Ng D, Niinemets Ü, O'Sullivan OS, Phillips OL, Poorter L, Poot P, Prentice IC, Salinas N, Rowland LM, Ryan MG, Sitch S, Slot M, Smith NG, Turnbull MH, VanderWel MC, Valladares F, Veneklaas EJ, Weerasinghe LK, Wirth C, Wright IJ, Wythers KR, Xiang J, Xiang S, Zaragoza-Castells J. 2015. Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist* **206**: 614-636, doi:10.1111/nph.13253

Baskaran P, Hyvonen R, Berglund SL, Clemmensen KE, Agren GI, Lindahl BD, Manzoni S. 2017. Modelling the influence of ectomycorrhizal decomposition on plant nutrition and soil carbon sequestration in boreal forest ecosystems. *New Phytologist* **213**: 1452–1465, doi: 10.1111/nph.14213

Bernacchi CJ, Singsaas EL, Pimentel C, Portis AR, Long SP. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell and Environment* **24**: 253-259, https://doi.org/10.1111/j.1365-3040.2001.00668.x

Bonan GB, Williams M, Fisher RA, Oleson KW. 2014. Modeling stomatal conductance in the earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum. *Geoscientific Model Development* **7**: 2193-2222, doi: 10.5194/gmd-7-2193-2014

Borer ET, Harpole WS, Adler PB, Lind EM, Orrock JL, Seabloom EW, Smith MD. 2014. Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution* **5**: 65–73, doi: 10.1111/2041-210X.12125

Brodribb TJ. 2009. Xylem hydraulic physiology: The functional backbone of terrestrial plant productivity. *Plant Science* **177**: 245-251.

Brzostek ER, Fisher JB, Phillips RP. 2014. Modeling the carbon cost of plant nitrogen acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. *Journal of Geophysical Research - Biogeosciences* **119**: 1684–1697, doi:10.1002/2014JG002660

Buckley TN, John GP, Scoffoni C, Sack L. 2015. How does leaf anatomy influence water transport outside the xylem? *Plant Physiology* **168**: 1616–1635.

Caldararu S, Purves DW, Palmer PI. 2014. Phenology as a strategy for carbon optimality: A global model. *Biogeosciences* **11**: 763-778, doi: 10.5194/bg-11-763-2014

Chen JL, Reynolds JF, Harley PC, Tenhunen JD. 1993. Coordination theory of leaf nitrogen distribution in a canopy. *Oecologia* **93,** 63–69, https://doi.org/10.1007/BF00321192

Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloway J, Heimann M, Jones C, Le Quéré C, Myneni RB, Piao S, Thornton P. 2013. Carbon and other biogeochemical cycles. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds.). (Cambridge University Press), pp 465-570.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Knox KJE. 2013. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist* **197**: 19-35, doi:10.1111/nph.12001

Collatz GJ, Ball JT, Grivet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* **54**: 107-136, doi: 10.1016/0168-1923(91)90002-8

Collier N, Hoffman FM, Lawrence DM, Keppel-Aleks G, Koven CD, Riley W J, Mu M, Randerson JT. 2018. The International Land Model Benchmarking (ILAMB) system: Design, theory, and implementation. *Journal of Advances in Modeling Earth Systems* **10**: 2731– 2754, https://doi.org/10.1029/2018MS001354

Cowan I, Farquhar G. 1977. Stomatal function in relation to leaf metabolism and environment: Stomatal function in the regulation of gas exchange. *Symposia of the Society for Experimental Biology* **31**: 471-505.

Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**: 341-344, doi: 10.1038/nature11882

Cui E, Huang K, Arain MA, Fisher JB, Huntzinger DN, Ito A, Luo Y, Jain AK, Mao J, Michalak AM, Niu S, Parazoo NC, Peng C, Peng S, Poulter B, Ricciuto DM, Schaefer KM, Schwalm CR, Shi X, Tian H, Wang W, Wang J, Wei Y, Yan E, Yan L, Zeng N, Zhu Q, Xia J. 2019. Vegetation functional properties determine uncertainty of simulated ecosystem productivity: A traceability analysis in the East Asian Monsoon Region. *Global Biogeochemical Cycles* **33**: 668-689, doi: 10.1029/2018gb005909

Damour G, Simonneau T, Cochard H, Urban L, 2010. An overview of models of stomatal conductance at the leaf level. *Plant Cell Environment* **33**, 1419–1438, doi: 10.1111/j.1365-3040.2010.02181.x

Deans RM, Brodribb TJ, Busch FA, Farquhar GD. 2020. Optimization can provide the fundamental link between leaf photosynthesis, gas exchange and water relations. *Nature Plants* **6**: 1116-1125, doi: 10.1038/s41477-020-00760-6

De Kauwe MG, Kala J, Lin YS, Pitman AJ, Medlyn BE, Duursma RA, Abramowitz G, Wang YP, Miralles DG. 2015. A test of an optimal stomatal conductance scheme within the CABLE land surface model. *Geoscientific Model Development* **8**: 431-452, doi: 10.5194/gmd-8-431-2015

Dewar R, Mauranen A, Mäkelä A, Hölttä T., Medlyn B., Vesala T. 2018. New insights into the covariation of stomatal, mesophyll and hydraulic conductances from optimization models incorporating nonstomatal limitations to photosynthesis. *New Phytologist* **217**: 571-585, doi: 10.1111/nph.14848

Dong N, Prentice IC, Evans BJ, Caddy-Retalic S, Lowe AJ, Wright IJ. 2017. Leaf nitrogen from first principles: field evidence for adaptive variation with climate. *Biogeosciences* **14**: 481–495, doi: 10.5194/bg-14-481-2017.

Dong, N., Prentice IC, Wright IJ, Evans BJ, Togashi HF, Caddy-Retalic S, McInerney FA, Sparrow B, Leitch E, Lowe AJ. 2020. Components of leaf-trait variation along environmental gradients. *New Phytologist* **228**: 82-94, https://doi.org/10.1111/nph.16558.

Dongsansuk A, Lütz C, Neuner G. 2013. Effects of temperature and irradiance on quantum yield of PSII photochemistry and xanthophyll cycle in a tropical and a temperate species. *Photosynthetica* **51**: 13–21, doi: 10.1007/s11099-012-0070-2

Drake, J. E., Power, S. A., Duursma, R. A., Medlyn, B. E., Aspinwall, M. J., Choat, B., Creek D, Eamus D, Maier C, Pfautsch S, Smith RA, Tjoelker MG, Tissue DT. 2017. Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: A comparison of model formulations. *Agricultural and Forest Meteorology* **247**: 454–466, doi: 10.1016/j.agrformet.2017.08.026

Dreyer E, Roux XL, Montpied P, Daudet FA, Masson F. 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiology* **21**: 223–232.

Ehleringer J, Pearcy RW. 1983. Variation in quantum yield for CO_2 uptake among C_3 and C_4 plants. *Plant Physiology* **73**: 555–559.

Eller CB, Rowland L, Mencuccini M, Rosas T, Williams K, Harper A, Medlyn BE, Wagner Y, Klein T, Teodoro GS, Oliveira RS, Matos IS, Rosado BHP, Fuchs K, Wohlfahrt G, Montagnani L, Meir P, Sitch S, Cox PM. 2020. Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate. *New Phytologist* **226**: 1622-1637, doi: 10.1111/nph.16419

Eller CB, Rowland L, Oliveira RS, Bittencourt PRL, Barris FV, da Costa ACL, Meir P, Friend AD, Mencuccini M, Sitch S, Cox P. 2018. Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics. *Philosophical Transactions of the Royal Society* B **373**: 20170315, doi: 10.1098/rstb.2017.0315

Falster DS, Brännström Å, Westoby M, Dieckmann U. 2017. Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences* **114**: E2719–E2728.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**: 78-90, doi: 10.1007/BF00386231

Farrior CE, Tilman D, Dybzinski R, Reich PB, Levin SA, Pacala SW. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. *Ecology* **94**: 2505-2517, doi: 10.1890/12-1548.1

Field C, Mooney HA. 1986. The photosynthesis-nitrogen relationship in wild plants. In T. Givnish (ed) *On the Economy of Plant Form and Function*. Cambridge University Press, pp 25-55.

Fisher JB, Huntzinger DN, Schwalm CR, Sitch S. 2014. Modeling the terrestrial biosphere. *Annual Review of Environment and Resources* **39**: 91-123, doi: 10.1146/annurev-environ-012913-093456

Fisher RA, Koven CD. 2020. Perspectives on the future of Land Surface Models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems* **12:** e2018MS001453, doi: 10.1029/2018MS001453

Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ, Lichstein JW, Longo M, Matheny AM, Medvigy D, Muller-Landau HC, Powell TL, Serbin SP, Sato H, Shuman JK, Smith B, Trugman AT, Viskari T, Verbeeck H, Weng E, Xu C, Xu X, Zhang T, Moorcroft PR. 2018. Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology* **24**: 35–54, doi: 10.1111/gcb.13910

Forkel M, Andela N, Harrison SP, Lasslop G, van Marle M, Chuvieco E, Dorigo W, Forrest M, Hantson S, Heil A, Li F, Mangeon S, Melton J, Sitch S, Yue C, Arneth A. 2019. Emergent relationships with respect to burned area in global satellite observations and fire-enabled vegetation models. *Biogeosciences* **16**: 57-76, https://doi.org/10.5194/bg-16-57-2019

Franklin O, Harrison SP, Dewar R, Farrior CE, Brännström A, Dieckmann U, Pietsch S, Falster D, Cramer W, Loreau M, Wang H, Mäkelä A, Rebel KT, Meron E, Schymanski SJ, Rovenskaya E, Stocker BD, Zaehle S, Manzoni S, van Oijen M, Wright IJ, Ciais P, van Bodegom P, Penuelas J, Hofhansl F, Terrer C, Soudzilovskaia NA, Midgley G, Prentice IC. **2020**. Organizing principles for vegetation dynamics. *Nature Plants* **6:** 444-453, doi: 10.1038/s41477-020-0655-x

Franklin O, McMurtrie RE, Iversen CM, Crous KY, Finzi AC, Tissue DT, Ellsworth DS, Oren R, Norby RJ. 2009. Forest fine-root production and nitrogen use under elevated CO_2: Contrasting responses in evergreen and deciduous trees explained by a common principle. *Global Change Biology* **15**: 132–144.

Franklin O, Näsholm T, Högberg P, Högberg MN. 2014. Forests trapped in nitrogen limitation – an ecological market perspective on ectomycorrhizal symbiosis. *New Phytologist* **203**: 657-666, doi: 10.1111/nph.12840

Friedlingstein P, Cox P, Betts R, Bopp L, Von Bloh W, Brovkin V, Cadule P, Doney S. Eby M, Fung I, Bala G, John J, Jones C. Joos F, Kato T, Kawamiya M, Knorr W, Lindsay K, Matthews D, Raddatz T, Payner P, Reick C, Roeckner E, Schnitzler K-G, Schnur R, Strassmann K, Weaver AJ, Yoshikawa C, Zeng N. 2006. Climate–carbon cycle feedback analysis: Results from the C^4MIP model intercomparison. *Journal of Climate* **19**: 3337–3353.

Friedlingstein P, O'Sullivan M, Jones MW, Andrew RM, Hauck J, Olsen A, Peters GP, Peters W, Pongratz J, Sitch S, Le Quéré C, Canadell JG, Ciais P, Jackson RB, Alin S, Aragão LEOC, Arneth A, Arora V, Bates NR, Becker M, Benoit-Cattin A, Bittig HC, Bopp L, Bultan S, Chandra N, Chevallier F, Chini LP, Evans W, Florentie L, Forster PM, Gasser T, Gehlen M, Gilfillan D, Gkritzalis T, Gregor L, Gruber N, Harris I, Hartung K, Haverd V, Houghton RA, Ilyina T, Jain AK, Joetzjer E, Kadono K, Kato E, Kitidis V, Korsbakken JI, Landschützer P, Lefèvre N, Lenton A, Lienert S, Liu Z, Lombardozzi D, Marland G, Metzl N, Munro DR, Nabel JEMS, Nakaoka S-I, Niwa Y, O'Brien K, Ono T, Palmer PI, Pierrot D, Poulter B, Resplandy L, Robertson E, Rödenbeck C, Schwinger J, Séférian R, Skjelvan I, Smith AJP, Sutton AJ, Tanhua T, Tans PP, Tian H, Tilbrook B, van der Werf G, Vuichard N, Walker AP, Wanninkhof R, Watson AJ, Willis D, Wiltshire AJ, Yuan W, Yue X, Zaehle S. 2020. Global Carbon Budget 2020. *Earth System Science Data* **12**: 3269-3340, doi: 10.5194/essd-12-3269-2020

Fyllas N, Gloor E, Mercado LM, Sitch S, Quesada CA, Domingues TF, Galbraith DR, Torre-Lezama A, Vilanova E Ramirez-Angulo H, Higuchi N, Neill DA, Silveira M, Ferreira L, Aymard CGA, Malhi Y, Phillips OL, Lloyd J. 2014. Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v. 1). *Geoscientific Model Development* **7**, 1251–1269, doi: 10.5194/gmd-7-1251-2014

Galmés J, Hermida-Carrera C, Laanisto L, Niinemets U. 2016. A compendium of temperature responses of Rubisco kinetic traits: variability among and within photosynthetic groups and impacts on photosynthesis modeling. *Journal of Experimental Botany* **67**: 5067–5091.

Galmés J, Kapralov MV, Copolovici LO, Hermida-Carrera C, Ninnemets U. 2015. Temperature responses of the Rubisco maximum carboxylase activity across domains of life: phylogenetic signals, trade-offs, and importance for carbon gain. *Photosynthesis Research* **123**: 183–201.

Gill AL, Finzi AC. 2016. Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecological Letters* **12**: 1419–1428, doi: 10.1111/ele.12690

Gramelsberger G, Lenhard J, Parker WS. 2020. Philosophical perspectives on Earth system modeling: Truth, adequacy, and understanding. *Journal of Advances in Modeling Earth Systems* **12**: e2019MS001720, doi: 10.1029/2019MS001720

Graven H, Keeling RF, Piper SC, Patra PK, Stephens BB, Wofsy SC, Welp LR, Sweeney C, Tans PP, Kelley JJ, Daube BC, Kort EA, Santoni GW, Bent JD. 2013. Enhanced seasonal exchange of CO_2 by northern ecosystems since 1960. *Science* **341**: 1085-1089, doi: 10.1126/science.1239207

Guenther A, Karl T, Harley P, Wiedinmyer C, Palmer PI, Geron C. 2006. Estimates of global terrestrial isoprene emissions using MEGAN (Model of Emissions of Gases and Aerosols from Nature. *Atmospheric Chemistry and Physics* **6**: 3181-3210, doi:10.5194/acp-6-3181-2006

Hantson S, Kelley DI, Arneth A, Harrison SP, Archibald S, Bachelet D, Forrest M, Kloster S, Lasslop G, Li F, Mangeon S, Melton JR, Nieradzik L, Rabin SS, Prentice IC, Sheehan T, Sitch S, Teckentrup L, Voulgarakis A, Yue C. 2020. Quantitative assessment of fire and vegetation properties in historical simulations with fire-enabled vegetation models from the FireMIP intercomparison project. *Geoscientific Model Development* **13**: 3299-3318, https://doi.org/10.5194/gmd-13-3299-2020

Harrison SP, **Sanchez Goñi MF, 2010**. Global patterns of vegetation response to millennial-scale variability during the last glacial: A synthesis. *Quaternary Science Reviews* 29: 2957-2980.

Harrison SP, Morfopoulos C, Dani KG, Prentice IC, Arneth A, Atwell BJ, Barkley MP, Leishman MR, Loreto F, Medlyn BE, Niinemets Ü, Possell M, Peñuelas J, Wright IJ. 2013. Volatile isoprenoid emissions from plastid to planet. *New Phytologist* **197**: 49-57. doi: 10.1111/nph.12021

Held IM. 2005. The gap between simulation and understanding in climate modeling. *Bulletin of the American Meteorological Society* **86**: 1609-1614, doi: 10.1175/BAMS-86-11-1609

Heskel MA, O'Sullivan OS, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Egerton JJG, Creek D, Bloomfield KJ, Xiang J, Sinca F, Stangl ZR, Martinez-de la Torre A, Griffin KL, Huntingford C, Hurry V, Meir P, Turnbull MH, Atkin OK. 2016. Convergence in the temperature response of leaf respiration across biomes and plant functional types. *Proceedings of the National Academy of Sciences* **113**: 3832-3837, doi: 10.1073/pnas.1520282113

Hilton TW, Loik ME, Campbell JE. 2019. Simulating International Drought Experiment field observations using the community land model. *Agricultural and Forest Meteorology* **266-267**: 173-183, doi: 10.1016/j.agrformet.2018.12.016

Hoeppner SS, Dukes JS. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology* **18**: 1754–1768, doi: 10.1111/j.1365-2486.2011.02626.x

Hovenden MJ, Leuzinger S, Newton PCD, Fletcher A, Fatichi S, Lüscher A, Reich PB, Andresen LC, Beier C, Blumenthal DM, Chiariello NR, Dukes JS, Kellner J, Hofmockel K, Niklaus PA, Song J, Wan S, Classen AT, Adam LJ. 2019. Globally consistent influences of seasonal precipitation limit grassland biomass response to elevated CO_2. *Nature Plants* **5**: 167–173, doi: 10.1038/s41477-018-0356-x

Huntingford C, Atkin OK, Martinez-de la Torre A, Mercado, LM, Heskel MaryA, Harper AB, Bloomfield KJ, O'Sullivan OS, Reich PB, Wythers KR, Butler, EE, Chen M, Griffin KL, Meir P, Tjoelker MG, Turnbull MH, Sitch S, Wiltshire A, Malhi Y. 2017. Implications of improved representations of plant respiration in a changing climate. *Nature Communications* **8**: 1602, doi: 10.1038/s41467-017-01774-z

Huntzinger DN, Michalak AM, Schwalm C, Ciais P, King AW, Fang FY, Schaefer K, Wei Y, Cook RB, Fisher JB, Hayes D, Huang M, Ito A, Jain AK, Lei H, Lu C, Maignan F, Mao J, Parazoo N, Peng S, Poulter B, Ricciuto D, Shi X, Tian H, Wang W, Zeng N, Zhao F. 2017. Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions. *Scientific Reports* **7**: 4765, doi: 10.1038/s41598-017-03818-2

Inoue Y, Ichie T, Kenzo T, Yoneyama A, Kumagai T, Nakashizuka T. 2017. Effects of rainfall exclusion on leaf gas exchange traits and osmotic adjustment in mature canopy trees of *Dryobalanops aromatica* (Dipterocarpaceae) in a Malaysian tropical rain forest. *Tree Physiology* **37**: 1301-1311, doi: 10.1093/treephys/tpx053

Joshi J, Stocker BD, Hofhansl F, Zhou S, Dieckmann U, Prentice IC. 2020. Towards a unified theory of plant photosynthesis and hydraulics. *bioRxiv* 2020.12.17.423132, doi: 10.1101/2020.12.17.423132

Kattge J*, et al,* 2020. Twelve years of TRY – towards a third generation of plant trait data assimilation and sharing. *Global Change Biology* **26**: 119-188, doi: 10.1111/gcb.14904

Keenan TF, Prentice IC, Canadell JG, Williams CA, Wang H, Raupach M, Collatz GJ. 2016. Recent pause in the growth rate of atmospheric CO_2 due to enhanced terrestrial carbon uptake. *Nature Communications* **7**: 13428, doi: 10.1038/ncomms13428

Kikuzawa K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *The American Naturalist* **138**: 1250-1263, doi: 10.1086/285281

Klein Goldewijk K, Beusen A, Doelman J, Stehfest E. 2017. Anthropogenic land-use estimates for the Holocene; HYDE 3.2. *Earth System Science Data* **9**: 927–953, https://doi.org/10.5194/essd- 9-927-2017

Knapp AK, Avolio ML, Beier C, Carroll CJW, Collins SL, Dukes JS, Fraser LH, Griffin-Nolan RJ, Hoover DL, Loik ME, Phillips RP, Post AK, Sala OE, Slette IJ, Yahdjian L, Smith MD. 2017. Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. *Global Change Biology* **23**: 1774-1782, doi: 10.1111/gcb.13504

Körner C, Diemer M. 1987. In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology* **1**: 179-194.

Kumarathunge DP, Medlyn BE, Drake JE, Tjoelker MG, Aspinwall MJ, Battaglia M, Cano FJ, Carter KR, Cavaleri MA, Cernusak LA, Chambers JQ, Crous KY, De Kauwe MG, Dillaway DN, Dreyer E, Ellsworth DS, Ghannoum O, Han Q, Hikosaka K, Jensen AM, Kelly JWG, Kruger EL, Mercado LM, Onoda Y, Reich PB, Rogers A, Slot M, Smith NG, Tarvainen L, Tissue DT, Togashi HF, Tribuzy ES, Uddling J, Vårhammar A, Wallin G, Warren JM, Way DA. 2019. Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale. *New Phytologist* **222**: 768-784, doi:10.1111/nph.15668

Kvakić M, Tzagkarakis G, Pellerin S, Ciais P, Goll D, Mollier A, Ringeval B. 2020. Carbon and phosphorus allocation in annual plants: an optimal functioning approach. *Frontiers in Plant Science* **11**: 149, doi: 10.3389/fpls.2020.00149

Lantz AT, Allman J, Weraduwage SM, Sharkey TD. 2019. Isoprene: New insights into the control of emission and mediation of stress tolerance by gene expression. *Plant Cell and Environment* **42**: 2808-2826, doi: 10.1111/pce.13629

Lavergne A, Voelker S, Csank A, Graven H, de Boer HJ, Daux V, Robertson I, Dorado-Liñán I, Martínez-Sancho E, Battipaglia G, Bloomfield KJ, Still CJ, Meinzer FC, Dawson TE, Camarero JJ, Clisby R, Fang Y, Menzel A, Keen RM, Roden JS, Prentice IC. 2020. Historical changes in the stomatal limitation of photosynthesis: empirical support for an optimality principle. *New Phytologist* **225**: 2484-2497, doi: 10.1111/nph.16314

Lavergne A, Sandoval D, Hare VJ, Graven H, Prentice, IC. 2020b. Impacts of soil water stress on the acclimated stomatal limitation of photosynthesis: insights from stable carbon isotope data., *Global Change Biology* **26**: 7158– 7172. https://doi.org/10.1111/gcb.15364

Lawrence DM, Fisher RA, Koven CD, Oleson KW, Swenson SC, Bonan G, Collier N, Ghimire B, van Kampenhout L, Kennedy D, Kluzek E, Lawrence PJ, Li F, Li H, Lombardozzi D, Riley WJ, Sacks WJ, Shi M, Vertenstein M, Wieder WR, Xu C, Ashehad AA, Badger AM, Bisht G, van den Broeke M, Brunke MA, Burns SP, Buzan J, Clark M, Craig A, Dahlin K, Drewniak B, Fisher JB, Flanner M, Fox AM, Gentine P, Hoffman F, Keppel-

Aleks G, Knox R, Kumar S, Lenaerts J, Leung LR, Lipscomb WH, LY Y, Pandey A, Pelletier JD, Perket J, Randerson JT, Ricciuto DM, Sanderson BM, Slater A, Subin ZM, Tang J, Thomas RQ, Martin MV, Zeng X. 2019. The Community Land Model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems* **11**: 4245– 4287, https://doi.org/10.1029/2018MS001583

Lin Y-S, Medlyn BE, Duursma RA, Prentice IC, Wang H, Baig S, Eamus D, de Dios VR, Mitchell P, Ellsworth DS, de Beeck MO, Wallin G, Uddling J, Tarvainen L, Linderson M-L, Cernusak LA, Nippert JB, Ocheltree TW, Tissue DT., Martin-StPaul NK, Rogers A, Warren JM, De Angelis P, Hikosaka K, Han Q, Onoda Y, Gimeno TE, Barton CVM, Bennie J, Bonal D, Bosc A, Löw M, Macinins-Ng C, Rey A, Rowland L, Setterfield SA, Tausz-Posch S, Zaragoza-Castells J, Broadmeadow MSJ, Drake JE, Freeman M, Ghannoum O, Hutley LB, Kelly JW, Kikuzawa K, Kolari P, Koyama K, Limousin J-M, Meir P, Lola da Costa AC, Mikkelsen TN, Salinas N, Sun W, Wingate L. 2015. Optimal stomatal behaviour around the world. *Nature Climate Change* **5**: 459-464, doi: 10.1038/nclimate2550

Lindh M, Zhang L, Falster D, Franklin O, Brännström Å. 2014. Plant diversity and drought: The role of deep roots. *Ecological Modelling* **290**: 85-93, doi: 10.1016/j.ecolmodel.2014.05.008

Locke AM, Sack L, Bernacchi CJ, Ort DR. 2013. Soybean leaf hydraulic conductance does not acclimate to growth at elevated [CO_2] or temperature in growth chambers or in the field. *Annals of Botany* **112**: 911–918, doi: 10.1093/aob/mct143

Longo M, Knox RG, Medvigy DM, Levine NM, Dietze MC, Kim Y, *et al.* 2019. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the Ecosystem Demography Model, Version 2.2—Part 1: Model description. *Geoscientific Model Development* **12**: 4309–4346, https://doi.org/10.5194/gmd-12-4309-2019

Lusk CH, Clearwater MJ, Laughlin DC, Harrison SP, Prentice IC, Nordenstahl M, Smith B. 2018. Frost and leaf-size gradients in forests: global patterns and experimental evidence. *New Phytologist* **29**: 565-573, doi: 10.1111/nph.15202

Maire V, Martre P, Kattge J, Gastal F, Esser G, Fontaine S, Soussana J-F. 2012. The coordination of leaf photosynthesis links C and N fluxes in C_3 plant species. *PLoS ONE* **7**: e38345, https://doi.org/10.1371/journal.pone.0038345

Manzoni S, Vico G, Thompson S, Beyer F, Weih M. 2015. Contrasting leaf phenological strategies optimize carbon gain under droughts of different duration. *Advances in Water Resources* **84**: 37–51, doi: 10.1016/j.advwatres.2015.08.001

Marchin RM, Broadhead AA, Bostic LE, Dunn RR, Hoffmann WA. 2016. Stomatal acclimation to vapour pressure deficit doubles transpiration of small tree seedlings with warming. *Plant, Cell & Environment* **39**: 2221– 2234, doi: 10.1111/pce.12790

Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, Barton CVM, Crous KY, De Angelis P, Freeman M, Wingate L. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology* **17**: 2134–2144, doi: 10.1111/j.1365-2486.2010.02375.x

Medlyn BE, Duursma RA, De Kauwe MG, Prentice IC. 2013. The optimal stomatal response to atmospheric CO_2 concentration: Alternative solutions, alternative interpretations. *Agriculture and Forest Meteorology* **182–183**: 200–203, doi: 10.1016/j.agrformet.2013.04.019

Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler T, Jain AK, Luo Y, Parton W, Prentice IC, Thornton PE, Wang S, Wang YP, Weng E, Iversen CM, McCarthy HR, Warren JM, Oren R, Norby RJ. 2015. Using ecosystem experiments to improve vegetation models. *Nature Climate Change* **5**: 528-534, doi: 10.1038/nclimate2621

Meng T-T, Wang H, Harrison SP, Prentice IC, Ni J, Wang G. 2015. Responses of leaf traits to climatic gradients: adaptive variation versus compositional shifts. *Biogeosciences* **12**: 5339-5352, doi: 10.5194/bg-12-5339-2015

Mengoli G, Agusti-Panareda A, Boussetta S, Harrison SP, Trotta C, Prentice IC. 2021. Ecosystem photosynthesis in land-surface models: a first-principles approach. Submitted to *Journal of Advances in Modeling Earth Systems*

Morfopoulos C, Prentice IC, Keenan TF, Friedlingstein P, Medlyn BE, Peñuelas J, Possell M. 2013. A unifying conceptual model for the environmental responses of isoprene emission by plants. *Annals of Botany* **112**: 1223-1238, doi: 10.1093/aob/mct206

Morfopoulos C, Sperlich D, Peñuelas J, Cubells JF, Llusià J, Medlyn BE, Possell M, Prentice IC. 2014. A model of plant isoprene emission based on available reducing power captures responses to atmospheric CO_2. *New Phytologist* **203**: 125-139, doi: 10.1111/nph.12770

Niinemets Ü. 2010. Mild versus severe stress and BVOCs: thresholds, priming and consequences. *Trends in Plant Science* **15**: 145–153.

Oliver RJ, Mercado LM, Sitch S, Simpson D, Medlyn BE, Lin Y-S, Folberth GA. 2018. Large but decreasing effect of ozone on the European carbon sink. *Biogeosciences* **15**: 4245–4269, doi: 10.5194/bg-15-4245-2018

Ostberg S, Boysen LR, Schaphoff S, Lucht W, Gerten D. 2018. The biosphere under potential Paris outcomes. *Earth's Future* **6**: 23-39, doi: 10.1002/2017EF000628

Pacifico F, Harrison SP, Jones CD, Arneth A, Sitch S, Weedon G, Barkley MP, Palmer PI, Serça D, Potosnak M, Fu T-M, Goldstein A, Bai J, Schurgers G. 2011. Evaluation of a photosynthesis-based biogenic isoprene emission scheme in JULES and simulation of isoprene emissions under present-day climate conditions. *Atmospheric Chemistry and Physics* **11**: 4371-4389, doi: 10.5194/acp-11-4371-2011

Paillassa J, Wright IJ, Prentice IC, Pepin S, Smith NG, Ethier G, Westerband AC, Lamarque LJ, Wang H, Cornwell WK, Maire V. 2020. When and where soil is important to modify the carbon and water economy of leaves. *New Phytologist* **228**: 121-135, https://doi.org/10.1111/nph.16702

Pastorello G, Trotta C, Canfora E, Chu H, Christianson D, Cheah YW, Poindexter C, Chen J, Elbashandy A, Humphrey M, Isaac P, Polidori D, Ribeca A, van Ingen C, Zhang L, Amiro B, Ammann C, Arain MA, Ardö J, Arkebauer T, Arndt SK, Arriga N, Aubinet M, Aurela M, Baldocchi D, Barr A, Beamesderfer E, Marchesini LB, Bergeron O, Beringer J, Bernhofer C, Berveiller D, Billesbach D, Black TA, Blanken PD, Bohrer G, Boike J, Bolstad PV, Bonal D, Bonnefond J-M, Bowling DR, Bracho R, Brodeur J, Brümmer C, Buchmann N, Burban B, Burns SP, Buysse P, Cale P, Cavagna M, Cellier P, Chen S, Chini I, Christensen TR, Cleverly J, Collalti A, Consalvo C, Cook BD, Cook D, Coursolle C, Cremonese E, Curtis PS, D'Andrea E, da Rocha H, Dai X, Davis KJ, De Cinti B, de Grandcourt A, De Ligne A, De Oliveira RC, Delpierre N, Desai AR, Di Bella, CM, di Tommasi P, Dolman H, Domingo F, Dong G, Dore S, Duce P, Dufrêne E, Dunn A, Dušek J, Eamus D, Eichelmann U, Elkhidir HAM, Eugster W, Ewenz CM, Ewers B, Famulari D, Fares S, Feigenwinter I, Feitz A, Fensholt R, Filippa G, Fischer M, Frank J, Galvagno M, Gharun M, Gianelle D, Gielen B, Gioli B, Gitelson A, Goded I, Goeckede M, Goldstein AH, Gough CM, Goulden ML, Graf A, Griebel A, Gruening C, Grünwald T, Hammerle A, Han S, Han X, Hansen BU, Hanson C, Hatakka J, He Y, Hehn M, Heinesch B, Hinko-Najera N, Hörtnagl L, Hutley L, Ibrom A, Ikawa H, Jackowicz-Korczynski M, Janouš D, Jans W, Jassal R, Jiang S, Kato T, Khomik M, Klatt J, Knohl A, Knox S, Kobayashi H, Koerber G, Kolle O, Kosugi Y, Kotani A, Kowalski A, Kruijt B, Kurbatova J, Kutsch WL, Kwon H, Launiainen S, Laurila T, Law B, Leuning R, Li

Y, Liddell M, Limousin J-M, Lion M, Liska AJ, Lohila A, López-Ballesteros A, López-Blanco E, Loubet B, Loustau D, Lucas-Moffat A, Lüers J, Ma S, Macfarlane C, Magliulo V, Maier R, Mammarella I, Manca G, Marcolla B, Margolis HA, Marras S, Massman W, Mastepanov M, Matamala R, Matthes JH, Mazzenga F, McCaughey H, McHugh I, McMillan AMS, Merbold L, Meyer W, Meyers T, Miller SD, Minerbi S, Moderow U, Monson RK, Montagnani L, Moore CE, Moors E, Moreaux V, Moureaux C, Munger JW, Nakai T, Neirynck J, Nesic Z, Nicolini G, Noormets A, Northwood M, Nosetto M, Nouvellon Y, Novick K, Oechel W, Olesen JE, Ourcival J-M, Papuga SA, Parmentier F-J, Paul-Limoges E, Pavelka M, Peichl MM, Pendall E, Phillips RP, Pilegaard K, Pirk N, Posse G, Powell T, Prasse H, Prober SM, Rambal S, Rannik Ü, Raz-Yaseef N, Reed D, de Dios VR, Restrepo-Coupe N, Reverter BR, Roland, M, Sabbatini, S, Sachs, T, Saleska, SR, Sánchez-Cañete, EP, Sanchez-Mejia ZM, Schmid HP, Schmidt M, Schneider K, Schrader F, Schroder I, Scott RL, Sedlák P, Serrano-Ortíz P, Shao C, Shi P, Shironya I, Siebicke L, Šigut L, Silberstein R, Sirca C, Spano D, Steinbrecher R, Stevens RM, Sturtevant C, Suyker A, Tagesson T, Takanashi S, Tang Y, Tapper N, Thom J, Tiedemann F, Tomassucci M, Tuovinen J-P, Urbanski S, Valentini R, van der Molen M, van Gorsel E, van Huissteden K, Varlagin A, Verfaillie J, Vesala T, Vincke C, Vitale D, Vygodskaya N, Walker JP, Walter-Shea E, Wang H, Weber R, Westermann S, Wille C, Wofsy S, Wohlfahrt G, Wolf S, Woodgate W, Li Y, Zampedri R, Zhang J, Zhou G, Zona D, Agarwal D, Biraud S, Torn M, Papale D. 2020.The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. *Scientific Data* **7,** 225, https://doi.org/10.1038/s41597-020-0534-3

Pausas JG. 2019. Generalized fire response strategies in plants and animals. *Oikos* **128**: 147-153, https://doi.org/10.1111/oik.05907

Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Davis SD. 2016. Towards understanding resprouting at the global scale. *New Phytologist* **209**: 945-954.

Peng Y, Bloomfield KJ, Prentice IC. 2020. A theory of plant function helps to explain leaf-trait and productivity responses to elevation. *New Phytologist* **226**: 1274-1284, https://doi.org/10.1111/nph.16447

Peters W, van der Velde IR, van Schaik E, Miller JB, Ciais P, Duarte HF, van der Laan-Luijkx IT, van der Molen MK, Scholze M, Schaefer K, Vidale PL, Verhoef A, Wårlind D, Zhu D, Tans PP, Vaughn B, White JWC. 2018. Increased water-use efficiency and reduced CO_2 uptake by plants during droughts at a continental scale. *Nature Geosci*ences **11:** 744–748, doi: 10.1038/s41561-018-0212-7

Pettinari ML, Chuvieco E. 2016. Generation of a global fuel data set using the Fuel Characteristic Classification System. *Biogeosciences* **13**: 2061-2076, doi: 10.5194/bg-13-2061-2016

Pongratz J, Reick C, Raddatz T, Claussen M. 2008. A re- construction of global agricultural areas and land cover for the last millennium, Global Biogeochemical Cycles **22**: GB3018, https://doi.org/10.1029/2007GB003153

Prentice IC, Cowling SA. 2013. Dynamic global vegetation models. In S.A. Levin (ed.) *Encyclopedia of Biodiversity*, 2nd edition, **2**, pp. 607-689. Academic Press.

Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ. 2014. Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecology Letters* **17**: 82-91, doi: 10.1111/ele.12211

Prentice IC, Liang X, Medlyn BE, Wang YP. 2015. Reliable, robust and realistic: the three R's of next-generation land-surface modelling. *Atmospheric Chemistry & Physics* **15**: 5987-6005 doi: 10.5194/acp-15-5987-2015

Prentice IC, **Bondeau A, Cramer W, Harrison SP, Hickler T, Lucht W, Sitch S, Smith B, Sykes MT. 2007.** Dynamic global vegetation modelling : quantifying terrestrial ecosystem responses to large-scale environmental change. In: J. Canadell, L. Pitelka and D. Pataki (eds) *Terrestrial Ecosystems in a Changing World*, Springer-Verlag, Berlin, pp. 175-192.

Quebbeman JA, Ramirez JA. 2016. Optimal allocation of leaf-level nitrogen: Implications for covariation of V_{cmax} and J_{cmax} and photosynthetic downregulation. *Journal of Geophysical Research Biogeosciences* **121**: 2464– 2475, doi:10.1002/2016JG003473

Qiao S, Wang H, Prentice IC, Harrison SP. 2020. Extending a generic primary production model to predict wheat yield. *Agriculture and Forest Meteorology* **287**, https://doi.org/10.1016/j.agrformet.2020.107932

Quillet A, Peng C, Garneau M. 2010. Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews*. **18**: 333-353, https://doi.org/10.1139/A10-016

Rastetter EB, Kwiatkowski BL. 2020. An approach to modeling resource optimization for substitutable and interdependent resources. *Ecological Modelling* **425**: 109033, doi: 10.1016/j.ecolmodel.2020.109033

Rastetter EB, Shaver GR. 1992. A model of multiple-element limitation for acclimating vegetation. Ecology 73: 1157-1174.

Reich PB, Luo Y, Bradford JB, Poorter H, Perry CH, Oleksyn J. 2014. Temperature drives forest biomass distribution. *Proceedings of the National Academy of Sciences* **111**: 13721-13726, doi: 10.1073/pnas.1216053111

Reichstein M, Bahn M, Mahecha MD, Kattge J, Baldocchi DD. 2014. Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences* **111**: 13697-13702, doi: 10.1073/pnas.1216065111

Rogers A, Belinda E. Medlyn BE, Dukes JS, Bonan G, von Caemmerer S, Dietze MC, Kattge J, Leakey ADB, Mercado LM, Niinemets Ü, Prentice IC, Serbin SP, Sitch S, Way DA, Zaehle S. 2017. A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytologist* **213**: 22-42, doi: 10.1111/nph.14283

Sabot MEB, de Kauwe MG, Pitman AJ, Medlyn BE, Verhoef A, Ukkola AM, Abramowitz G. 2020. Plant profit maximization improves predictions of European forest responses to drought. New Phytologist **226**: 1638-1655, doi: 10.1111/nph.16376

Sakschewski B, von Bloh W, Boit A, Rammig A, Kattge J, Poorter L, Peñuelas J, Thonicke K. 2015. Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology* **21**: 2711-2725, doi: 10.1111/gcb.12870

Scafaro AP, Xiang S, Long BM, Bahar NHA, Weerasinghe LK, Creek D, Evans JR, Reich PN, Atkin OK. 2017. Strong thermal acclimation of photosynthesis in tropical and temperate wet-forest tree species: the importance of altered Rubisco content. *Global Change Biology* **23**: 2783–2800, doi: 10.1111/gcb.13566

Shi M, Fisher JB, Brzostek ER, Phillips RP. 2016. Carbon cost of plant nitrogen acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the Community Land Model. *Global Change Biology* **22**: 1299–1314, 615 doi:10.1111/gcb.13131

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV, de L. Dantas V, de Bello F, Duarte LDS, Fonseca CR, Freschet GT, Gaucherand S, Gross N, Hikosaka K, Jackson B, Jung V, Kamiyama C, Katabuchi M, Kembel SW, Kichenin E, Kraft NJB, Lagerström A, Bagousse-Pinguet YL, Li Y, Mason N, Messier J, Nakashizuka T, Overton JM, Peltzer DA, Pérez-Ramos IM, Pillar VD, Prentice HC, Richardson S, Sasaki T, Schamp BS, Schöb C, Shipley B, Sundqvist M, Sykes MT, Vandewalle M, Wardle DA. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406-1419, doi: 10.1111/ele.12508

Singsaas EL, Ort DR, DeLucia EH. 2001. Variation in measured values of photosynthetic quantum yield in ecophysiological studies. *Oecologia* **128**: 15–23, doi: 10.1007/s004420000624

Smith NG, Dukes JS. 2017. LCE: leaf carbon exchange data set for tropical, temperate, and boreal species of North and Central America. *Ecology* **98**: 2978–2978, doi: 10.1002/ecy.1992

Smith NG, Dukes JS. 2018. Drivers of leaf carbon exchange capacity across biomes at the continental scale. *Ecology* **99**: 1610–1620, doi: 10.1002/ecy.2370

Smith NG, Keenan TF, Prentice IC, Wang H, Wright IJ, Niinemets Ü, Crous Y, Domingues TF, Guerrieri R, Ishida FY, Kattge J, Kruger EL, Maire V, Rogers A, Serbin SP, Tarvainen L, Togashi HF, Townsend PA, Wang M, Weerasinghe LK, Zhou, S-X. 2019. Global photosynthetic capacity is optimized to the environment. *Ecology Letters* **22**: 506–517, doi: 10.1111/ele.13210

Sperry JS, Venturas MD, Anderegg WRL, Mencuccini M, Mackay DS, Wang Y, Love DM. 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant, Cell & Environment* **40**: 816–830, doi: 10.1111/pce.12852

Stocker BD, Wang H, Smith NG, Harrison SP, Keenan T, Sandoval D, Davis T, Prentice IC, 2020. P-model v1.0: An optimality-based light use efficiency model for terrestrial gross primary production. *Geoscientific Model Development* **13**: 1545-1581, doi: 10.5194/gmd-13-1545-2020

Sulman BN, Brzostek ER, Medici C, Shevliakova E, Menge DNL, Phillips RP. 2017. Feedbacks between plant N demand and rhizosphere priming depend on type of mycorrhizal association. *Ecology Letters* **20**: 1043-1053, doi: 10.1111/ele.12802

Sun Z, Hüve K, Vislap V, Niinemets Ü. 2013. Elevated [CO_2] magnifies isoprene emissions under heat and improces thermal resistance in hybrid aspen. *Journal of Experimental Botany* **64**: 5509-5523, doi: 10.1093/jxb/ert318

Taylor TC, McMahon SM, Smith MN, Boyle B, Violle C, van Haren J, Simova I, Meir P, Ferreira LV, de Camargo PB, da Costa ACL, Enquist BJ, Saleska SR. 2018. Isoprene emission structures tropical tree biogeography and community assembly responses to climate. *New Phytologist* **220**: 435-446, https://doi.org/10.1111/nph.15304

Terrer C, Vicca S, Stocker BD, Hungate BA, Phillips RP, Reich PB, Finzi AC, Prentice IC. 2018. Ecosystem responses to elevated CO_2 governed by plant–soil interactions and the cost of nitrogen acquisition. *New Phytologist* **217**: 507–522, doi: 10.1111/nph.14872

Thomas RB, Prentice IC, Graven H, Ciais P, Fisher JB, Huang M, Huntzinger DN, Ito A, Jacobson A, Jain A, Mao J, Michalak A, Peng S, Poulter B, Ricciuto DM, Shi X, Schwalm C, Tian H, Zeng N. 2016. Increased light-use efficiency in northern terrestrial ecosystems indicated by CO_2 and greening observations. *Geophysical Research Letters* **43**: 11339-11349.

Thomas RQ, Williams M. 2014. A model using marginal efficiency of investment to analyse carbon and nitrogen interactions in terrestrial ecosystems (ACONITE Version 1). *Geoscientific Model Development* **7**: 2015–2037, https://doi.org/10.5194/gmd-7-2015-2014

Togashi HF, Prentice IC, Atkin OK, Macfarlane C, Prober SM, Bloomfield KJ, Evans BJ. 2018a. Thermal acclimation of leaf photosynthetic traits to temperature in an evergreen woodland, consistent with the coordination hypothesis. *Biogeosciences* **15**: 3461-3474, doi: 10.5194/bg-15-3461-2018.

Togashi HF, Atkin OK, Bloomfield KJ, Bradford M, Cao K, Dong N, Evans BJ, Fan Z, Harrison SP, Hua Z, Liddell MJ, Lloyd J, Ni J, Wang H, Weerasingha LK, Prentice IC. 2018b. Functional trait variation related to gap dynamics in tropical moist forests: A vegetation modelling perspective. *Perspectives in Plant Ecology, Evolution and Systematics* **35**: 52-64, doi: 10.1016/j.ppees.2018.10.004

Tomasella M, Beikircher B, Häberle K-H, Hesse B, Kallenbach C, Matyssek R, Mayr S. 2018. Acclimation of branch and leaf hydraulics in adult *Fagus sylvatica* and *Picea abies* in a forest through-fall exclusion experiment. *Tree Physiology* **38**: 198-211, doi: 10.1093/treephys/tpx140

Tramontana G, Jung M, Schwalm CR, Ichii K, Camps-Valls G, Raduly B, Reichstein M, Arain MA, Cescatti A, Kiely G, Merbold L, Serrano-Ortiz P, Sickert S, Wolf S, Papale DJ. 2016. Predicting carbon dioxide and energy fluxes across global FLUXNET sites with regression algorithms. *Biogeosciences* **13**: 4291-4313 doi: 10.5194/bg-13-4291-2016

Trugman AT, Anderegg LDL, Sperry JS, Wang Y, Venturas M, Anderegg WRL. 2019. Leveraging plant hydraulics to yield predictive and dynamic plant leaf allocation in vegetation models with climate change. *Global Change Biology* **25**: 4008-4021, doi: 10.1111/gcb.14814

Ukkola AM, Prentice IC. 2013. A worldwide analysis of trends in water-balance evapotranspiration. *Hydrology & Earth System Science* **17**: 4177-4187, doi: 10.5194/hess-17-4177-2013

Valentine HT, Mäkelä A. 2012. Modeling forest stand dynamics from optimal balances of carbon and nitrogen. *New Phytologist* **194**: 961-971, doi: 10.1111/j.1469-8137.2012.04123.x

Van Bodegom PM, Douma JC, Witte JPM, Ordoñez JC, Bartholomeus RP, Aerts R. 2012. Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: Exploring the merits of traits-based approaches. *Global Ecology & Biogeography* **21**: 625-636, doi: 10.1111/j.1466-8238.2011.00717.x

Venturas MD, Sperry JS, Love DM, Frehner EH, Allred MG, Wang Y, Anderegg WRL. 2018. A stomatal control model based on optimization of carbon gain versus hydraulic risk predicts aspen sapling responses to drought. *New Phytologist* **220**: 836-850, doi: 10.1111/nph.15333

Verheijen LM, Aerts R, Brovkin V, Cavender-Bares J, Cornelissen JHC, Kattge J, van Bodegom PM. 2015. Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology* **21**: 3074-3086, doi: 10.1111/gcb.12871

Vico G, Way DA, Hurry V, Manzoni S. 2019. Can leaf net photosynthesis acclimate to rising and more variable temperatures? *Plant Cell Environment* **42**: 1913–1928, doi: 10.1111/pce.13525

Wang H, Atkin OK, Keenan TF, Smith NG, Wright IJ, Bloomfield KJ, Kattge J, Reich PB, Prentice IC. 2020. Acclimation of leaf respiration consistent with optimal photosynthetic capacity. *Global Change Biology* **26**: 2573–2583, doi: 10.1111/gcb.14980

Wang H, Prentice IC, Cornwell WM, Keenan TF, Davis TW, Wright IJ, Evans BJ, Peng C. 2017. Towards a universal model for carbon dioxide uptake by plants. *Nature Plants* **3**: 734-741, doi: 10.1038/s41477-017-0006-8

Wang H, Prentice IC, Davis TW. 2014. Biophysical constraints on gross primary production by the terrestrial biosphere. *Biogeosciences* **11**: 5987-6001, doi: 10.5194/bg-11-5987-2014

Wang Y, Sperry JS, Anderegg WRL, Venturas MD, Trugman AT. 2020. A theoretical and empirical assessment of stomatal optimization modeling. *New Phytologist* **227**: 311-325, doi:10.1111/nph.16572

Weng E, Farrior CE, Dybzinski R, Pacala SW. 2017. Predicting vegetation type through physiological and environmental interactions with leaf traits: Evergreen and deciduous forests in an Earth system modeling framework. *Global Change Biology* **23**: 2482–2498, https://doi.org/10.1111/gcb.13542

Wieder WR, Cleveland CC, Smith WK, Todd-Brown K. 2015. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geosciences* **8**: 441-444, doi: 10.1038/ngeo2413

Wieder WR, Lawrence DM, Fisher RA, Bonan GB, Cheng SJ, Goodale CL., Grandy AS, Koven CD, Lombardozzi DL, Oleson KW, Thomas RQ. 2019. Beyond static benchmarking: Using experimental manipulations to evaluate land model assumptions. *Global Biogeochemical Cycles* **33**: 1289–1309, doi: 10.1029/2018GB006141

Wolf A, Anderegg WRL, Pacala SW. 2016. Optimal stomatal behavior with competition for water and risk of hydraulic impairment. *Proceedings of the National Academy of Sciences* **113**: E7222-E7230, doi 10.1073/pnas.1615144113

Wright IJ, Reich P, Westoby M, Ackerly D, Baruch Z, Bongers F, Cavender-Bares J, Cornelissen J, Diemer M, Flexas J, Garnier E, Groom P, Gulias J, Hikosaka K, Lamont

B, Lee T, Lee W, Lusk C, Villar R. 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821-827, doi: 10.1038/nature02403

Xia J, Yuan W, Wang YP, Zhang Q. 2017. Adaptive carbon Allocation by plants enhances the terrestrial carbon sink. *Scientific Reports* **7,** 3341, https://doi.org/10.1038/s41598-017-03574-3

Xu H, Wang H, Prentice IC, Harrison SP, Wang G, Sun X. 2020. Predictability of leaf traits with climate and elevation: a case study in Gongga Mountain, China. *Tree Physiology* (in revision)

Xu X, Medvigy D, Wright JS, Kitajima K, Wu J, Albert LP, Martins GA, Saleska SR, Pacala SW. 2017. Variations of leaf longevity in tropical moist forests predicted by a trait driven carbon optimality model. *Ecology Letters* **20**: 1097-1106, doi: 10.1111/ele.12804

Yang J, Cao M, Swenson NG. 2018. Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution* **33**: 326-336, doi: 10.1016/j.tree.2018.03.003

Box: How land (vegetation?) models are developed: some problems and proposed solutions

Models do not encapsulate a coherent body of theory. Current models represent the accumulation of work by successive cohorts of scientists in a specific institution or collaboration. Generally, no one has a complete overview of what they contain, or why particular decisions were made in the past (Fisher and Koven, 2020). This approach is normal for operational (e.g. national weather or air-quality forecast) models, but it inhibits efforts to trace why a model behaves as it does. We suggest there is a need for a *re-design, in which the core processes are examined one-by-one* and specific hypotheses about these processes tested against relevant data. Our proposed theory-driven approach more closely resembles how models are used in most other fields of science.

Lack of clarity about hypotheses. Many aspects of plant and ecosystem function are subject to alternative interpretations, and it seems likely that some differences among the results of models originate in different hypotheses adopted for one or another process. These hypotheses are seldom explicitly stated, however. Although model codes and documentation are now commonly made public (a positive development), the models' complex history can make it hard to discern their underlying logic. There is a strong argument for greater clarity, and above all, a *re-examination of the evidence* underlying the representation of each process.

Unclear testing protocols. New process representations are often assessed by changing one component within an existing, complex model and examining the effect on model outputs. Results obtained in this way are seldom clear-cut, however, because they are potentially vitiated by errors elsewhere in the model. Instead, *model components should be tested independently of others*.

Core process representations tend to be conserved. In many vegetation models, representations of the core processes of coupled energy, carbon and water exchange have remained unchanged since their original formulation. There is, in principle, no reason why new representations of core processes should not replace existing ones. However, it is noteworthy that this has not generally happened. The "legacy" formulations were likely provisional, and might now be obsolete – yet they are seldom isolated and tested, while model "improvement" more often consists of adding new processes (Fisher et al. 2014). We propose that model development should be *re-focused on the critical analysis and evaluation of core process representations,* and new processes added only if evidence unambiguously shows that they are required.

Neglect of available observations. Model parameter estimation tends to be *ad hoc* and is frequently based on single values for 'model' species that are long outdated. Models are relatively uninformed by the wealth of currently available observations. This situation could be remedied by *closer integration of data analysis and experimental research* into model development.

Figure Captions

Figure 1. Response of photosynthetic capacity (V_{cmax}) measured in *Holcus lanatus* (C_3 grass) and *Solanum dulcamara* (vine) to CO_2, shown in growth-chamber experiments where ambient CO_2 and phosphorus (P) supply were manipulated (H. J. de Boer, unpublished results). Low-P and high-P treatments received fertilizer with nitrogen to phosphorus (N:P) ratios of 45:1 and 1:1, respectively. The responses of V_{cmax} to sub-ambient and elevated CO_2 are consistent with the predictions of the coordination hypothesis as modelled following the eco-evolutionary optimality formulations of Wang et al. (2014) (P14) and Smith et al. (2019) (S19). This response is not affected by nutrient supply (high- and low-P treatments). Experimental V_{cmax} was scaled relative to the high-P population average under ambient CO_2 growth conditions (450 ppm), whereas modelled V_{cmax} was scaled relative to the single 450 ppm prediction. The response to CO_2 is significant at the 99% confidence level, as is the response to P supply, but the interaction term is non-significant indicating that the response to CO_2 is the same regardless of P supply.

Figure 2. Observed (by eddy covariance, grey) and modelled (using the same parameter set, red) half-hourly gross primary production (GPP) during one week in August 2014 at sites in a tropical (GF-Guy) and a boreal (FI-HYY) forest. Grey bands denote the range of GPP calculated by alternative partitioning methods in the FLUXNET2015 database (Pastorello et al., 2020).

Figure 3. Field-measured (black lines) (a) leaf dark respiration rates (R_{dark}) and (b) photosynthetic capacities (V_{cmax}) compared to their modelled responses to growing-season temperature (red solid lines) as predicted by the coordination hypothesis (Wang et al., 2020). Both R_{dark} and V_{cmax} have been corrected (using the Arrhenius equation, with ΔH as provided by Bernacchi et al. 2001) from the specific measurement temperature to the growing-season average temperature for the site. The coordination hypothesis predicts acclimated responses to temperature. The red dashed lines show the *instantaneous* responses to temperature, i.e. the relationship assumed by most models, based on the same Arrhenius equation. Data from the GlobResp (Atkin et al., 2015) and LCE (Smith and Dukes, 2017) data sets.

Figure 4. Trends in the ratio of leaf-internal to ambient CO_2 reconstructed from stable carbon isotope ratios in tree rings for different sites (coloured lines) and for the whole dataset (black) with respect to (a) mean growth temperature, (b) vapour pressure deficit (VPD), (c) atmospheric CO_2 and (d) elevation, compared to modelled trends (red line) for the whole dataset based on the least-cost hypothesis. Data and model results from Lavergne et al. (2020a).

Figure 5. Observed relationships (black lines) between leaf lifespan and (a) leaf mass per area, (b) radiation and (c) growing-season length as a fraction of the year compared to relationships predicted

(red lines) by the time-averaged maximization of leaf carbon gain through leaf lifespan after accounting for construction costs (H. Wang, unpublished results). All values are shown on a log scale. Data from evergreen species in the GLOPNET trait database (Wright et al., 2004).

Figure 6. Observed photosynthesis (a) and isoprene emission (b) at University of Michigan Biological Station forest in relation to incident photosynthetic photon flux density (PPFD), compared to modelled values (red lines) based on the FvCB model and the hypothesis that isoprene emission is related to leaf energetic status (Morfopoulos et al., 2013). Data are shown for an air temperature range of 24.5-25℃ to limit impact of temperature on the response to PPFD. The black lines represent relationships of GPP and isoprene emission rate to changes in PPFD estimated by Michaelis-Menten type functions fitted to the data.

Figure 7. Comparison of observed against modelled (a) soil N availability, (b) tree N uptake, and (c) net primary production (NPP) under ambient (open symbols) and elevated (dark grey symbols) CO_2, and with nitrogen fertilization (light grey symbols), at two free-air carbon dioxide enrichment experiments: Duke FACE (circles) and ORNL FACE (squares). The plant-level optimality model optimizes canopy N, LAI, and fine-root production by maximizing net growth as a proxy for fitness. The imposed treatment effects (independent variables) are light-saturated leaf-level photosynthetic N-use efficiency and soil N availability (maximal potential N uptake per root C). The r^2 is 0.90 for NPP, and 0.85 for N uptake (excluding circled outliers). Measured units of soil N in (a) are extractable nitrate (0.1 μg g soil^{-1}) in Duke and net N mineralization (20 μg g soil^{-1} y^{-1}) in ORNL. Data and model results from Franklin et al. (2009).

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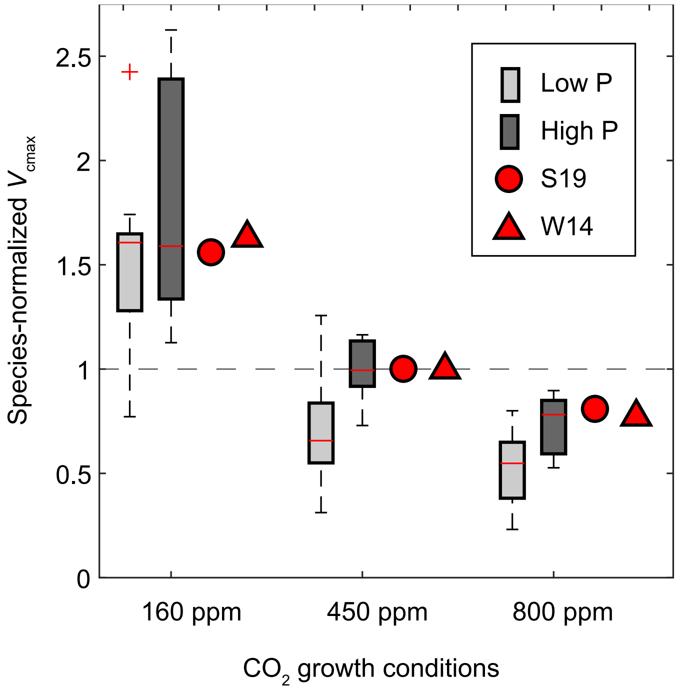

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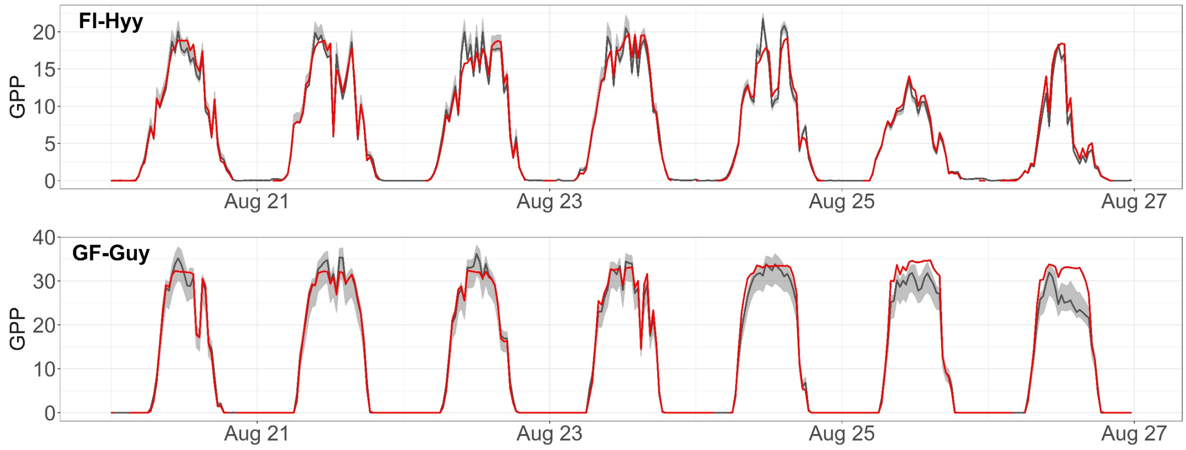
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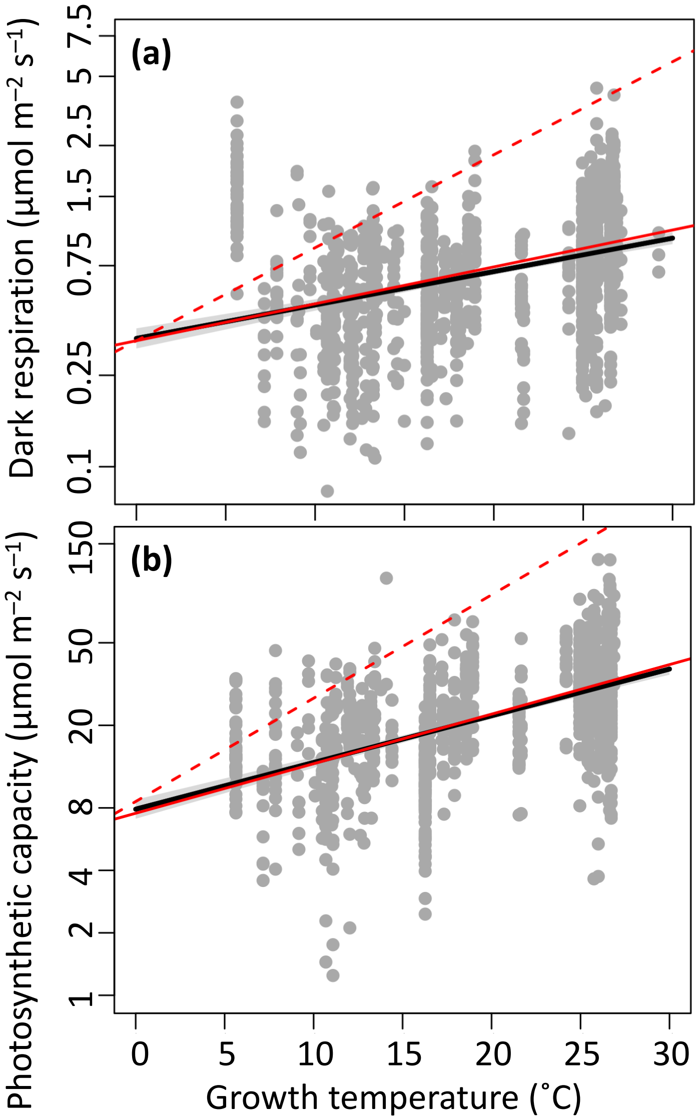

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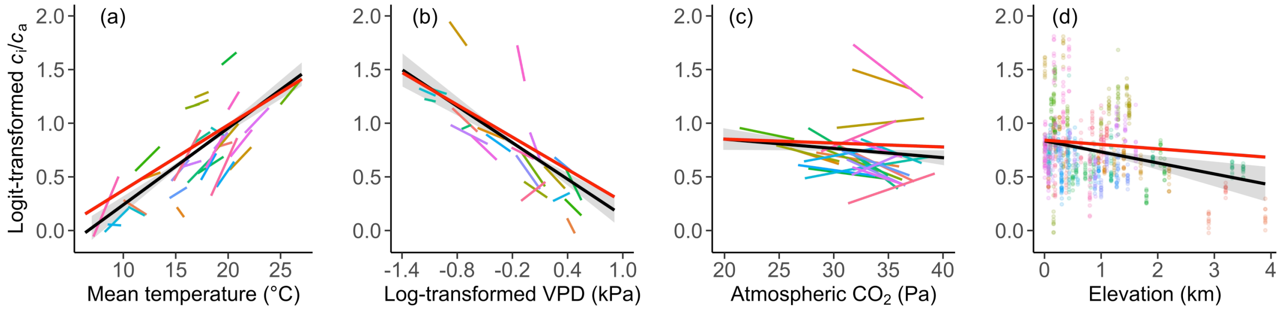

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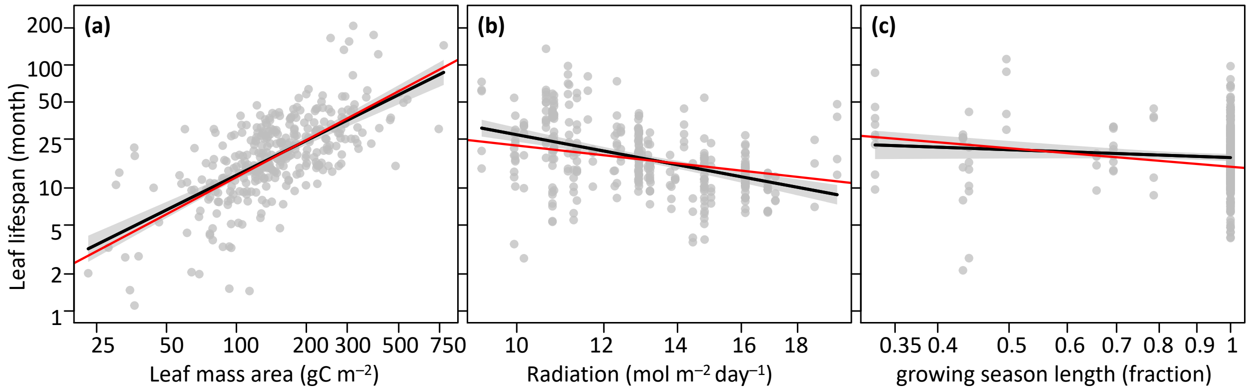

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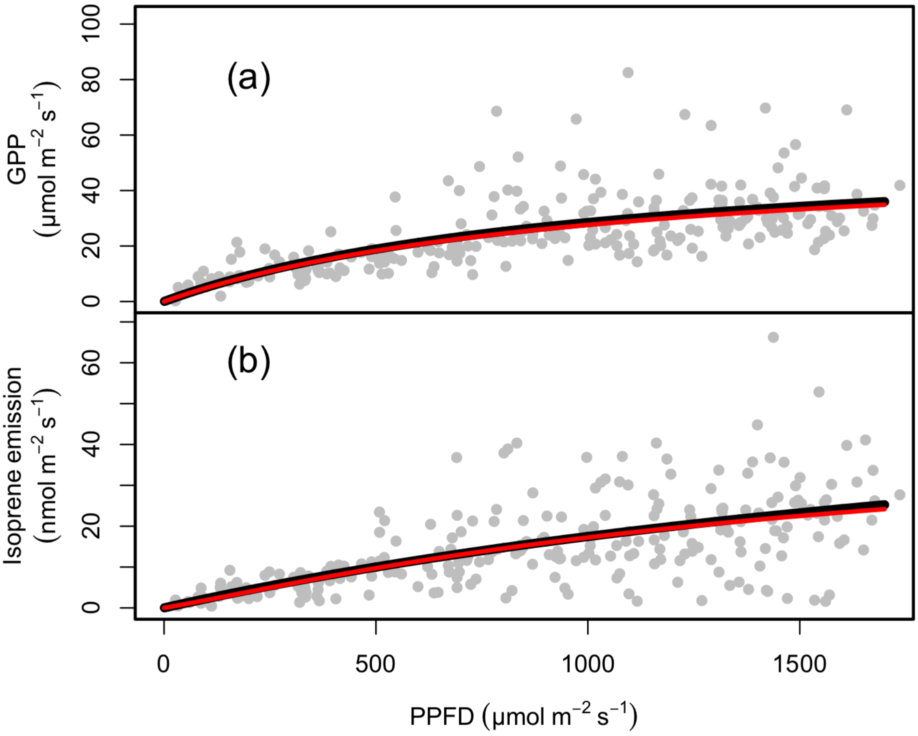

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