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

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Summary	190	**No of tables**	0
Introduction	1449	**No of boxes**	2
II. Model development: problems and solutions	715	**No of Supporting Information files**	1
III. Leaf-level and canopy-level optimality	2576		
IV. Beyond the leaf level	697		
V. Outstanding issues	1048		
VI. Concluding remarks	395		
Acknowledgements	360		

Contents

Summary

Global vegetation and land-surface models embody interdisciplinary scientific understanding of the behaviour of plants and ecosystems, and are indispensable to project the impacts of environmental change on vegetation and the interactions 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. In this review, focusing on core plant functions in the terrestrial carbon and water cycles, we show how unifying hypotheses derived from eco-evolutionary optimality (EEO) principles can provide novel, parameter-sparse representations of plant and vegetation processes. We present case studies that demonstrate how EEO generate parsimonious representations of core, leaf-level processes that are individually testable and supported by evidence. EEO approaches to photosynthesis and primary production, dark respiration, and stomatal behaviour are ripe for implementation in global models. EEO approaches to other important traits, including the leaf economics spectrum and applications of EEO at the community level are active research areas. Independently tested modules emerging from EEO studies 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. LSMs – with or without dynamic vegetation – provide the means for Earth System Models (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.

Process-based global vegetation models, including DGVMs and LSMs without dynamic vegetation, are based on explicit formulations of a set of processes rather than on observed relationships (in contrast, for example, with forest yield tables) and they use generic plant types (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. An ensemble of global vegetation models is used in the Global Carbon Project's annual update on the state of the carbon cycle (Friedlingstein et al., 2020). Model ensembles are widely used to assess the role of vegetation in land-atmosphere interactions, such as diagnosing the causes of fluctuations in the atmospheric CO_2 growth rate (Keenan et al., 2016). Vegetation models have also been used to quantify 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 investigate the impact of recent climate change on the hydrological cycle (e.g. Ukkola and Prentice, 2013), and to project 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 have tried 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 the $^{13}C/^{12}C$ ratio of atmospheric CO_2 and global land-atmosphere carbon exchange (Peters et al., 2018). There are persistent disagreements between models, 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 Intergovernmental Panel on Climate Change (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). However, finding ways to test alternative hypotheses using observations will mean 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 shape predictable, general patterns in vegetation structure and composition. The term 'eco-evolutionary’ expresses the fact that organisms adjust to their environment on both shorter (eco-physiological, days to months) timescales and longer (demographic and evolutionary) timescales.

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) is essential to understand 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, such as leaf mass per area (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, also 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.

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. Process-based vegetation models 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 hypotheses have shown a notable ability to predict observed patterns, providing parsimonious explanations of observed traits 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 must 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. Most models represent plant adaptations to environmental conditions by specifying a limited set of PFTs, each characterized by a distinct set of attributes. This is problematic 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). Furthermore, incorporation of new processes within this framework necessarily implies a proliferation of new PFTs and the necessity to derive estimates of parameter values for each new PFT. An alternative approach that has been gaining traction over the past decade has been towards the simulation of 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 (Reichstein et al., 2014; Sakschewski et al., 2015).

Several problems (see Box 1) 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 1). 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. 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 could have a key role to play because it can generate coherent, testable hypotheses about plant and vegetation function that transcend differences among biomes and floras.

III. Leaf-level and canopy-level optimality

In this section, we summarize a number of case studies that demonstrate where EEO approaches have provided parsimonious representations of core, leaf-level processes that are individually testable and supported by evidence. The 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.

Photosynthesis and primary production. Nearly all LSMs and DGVMs simulate photosynthesis using the Farquhar, von Caemmerer and Berry (FvCB) model (Farquhar et al., 1980) or the modification proposed by Collatz et al. (1991). Implementing the FvCB model in its original form requires three parameters that are known to vary: 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 that modify the assumed proportional relationship between gross primary production (GPP) and light absorbed by the canopy (I*abs*). This approach can limit the number of parameters to be estimated but severs the link to processes.

The model described in Box 2 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), seasonal variations of V_{cmax} across diverse ecosystems (Jiang et al., 2020), elevational trends in photosynthetic traits and primary production (Peng et al., 2020), and the response of V_{cmax} to atmospheric CO_2 (Smith and Keenan, 2020). 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 in Box 2 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 ξ, which 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.

This 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 a standard temperature (e.g. 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., 2021). Moreover, 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 R_{dark} and V_{cmax} with separate 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 EEO 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. 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} varies 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 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 LSMs (e.g. De Kauwe et al., 2015; Franks et al., 2018; Oliver et al., 2018) and shown to perform as well as the empirical relationships originally used in those models. 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 Cowan and Farquhar (CF) hypothesis by accounting for soil moisture dynamics in the optimization problem (Manzoni et al. 2013), 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) and summarized in Box 2, is based on the EEO hypothesis that leaves minimize the sum of the maintenance costs (per unit assimilation) of transpiration and carboxylation capacities. 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 closely related 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) showed a (weak) dependency of χ on atmospheric CO_2 (Figure 4) that is also predicted by this EEO hypothesis (Box 2). 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 EEO-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 the one "universal" parameter it includes 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; Deans et al., 2020; Joshi et al., 2020), and the influence of soil 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). The coordination between these two rates is what enables plants to optimise light use efficiency at low levels of irradiance and to dissipate excess energy as heat at high irradiance. The linear dependency on the energetic status 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 carbon allocation to leaves (Cui et al., 2019). The leaf economics spectrum (Wright et al., 2004) relates LMA and leaf lifespan (LL) across vascular plant species. 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. X. 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 directly proportional to V_{cmax25}; while the coordination hypothesis, described above, predicts optimal values of V_{cmax25}. Combining these three EEO hypotheses leads to a theoretical prediction of the leaf economics spectrum, and how it varies across environments (H. Wang et al., 2021). 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 (H. Wang et al., 2021; Figure 6). A changing climate will inevitably alter the competitive balance among species with different LMA and LL, in ways that fixed LMA values per PFT cannot capture.

In addition to affecting leaf lifespan, LMA mechanistically affects stomatal response (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 conservatism is helpful here. Starting from the observed global distributions of these traits, the model of H. Wang et al. (2021) calculates how these intersect with the predicted optimal LMA-LL relationship. This approach generates probability distributions around the predicted community-mean values as illustrated in Figure 6.

IV. Beyond the leaf level

Most published applications of EEO concepts in vegetation modelling have focused on leaf-level physiological processes, facilitated by their phenotypic plasticity and the short timescale of some leaf-level responses to environmental conditions. The EEO framework however extends naturally to phenotypic plasticity at 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. The EEO approach can be extended to non-plastic trait variation if selection on these traits is not strongly frequency-dependent, i.e. if the fitness of plants does not depend strongly on the frequency of traits among their conspecifics (Metz et al., 2008). EEO concepts are particularly powerful for describing trait coordination for example among different plant organs (Deans et al., 2020): when multiple traits optimally adapt to the environment, environmental variation leads to covariation between them. Such emergent relationships may provide the basis for modelling how evolved traits vary with environmental conditions without simulating the underlying physiological mechanisms (or evolutionary dynamics) through which optimal coordination is achieved. We briefly consider now the potential application of the EEO framework to modelling whole-plant processes, competition and ecosystem dynamics.

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 (Poorter et al., 2012; Reich et al., 2014; Gill and Finzi, 2016). This observation is consistent with the long-established EEO hypothesis that plants, requiring multiple resources, allocate effort optimally so that no one resource is limiting to growth (Rastetter and Shaver, 1992; Thomas and Williams, 2014; Rastetter and Kwiatkowski, 2020). 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).

Competition and coexistence. If the fitness of plants is strongly influenced by competition with other plants in a way that depends on the frequency of their traits, game-theoretic extensions of the EEO framework such as adaptive dynamics theory (Metz et al., 1992; Dieckmann and Law, 1996) can be used to predict not only single optimal plant strategies but also coexisting and co-evolving strategies. 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 realistic patterns of stable coexistence of tree species in a height-structured competition model related to the demographic schemes used in DGVMs. Other game-theoretic approaches (e.g. Dybzinski et al., 2015; Weng et al., 2019) have shown that co-existing strategies can give rise to emergent trait coordination, which can be compared with empirical observations. 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 very difficult 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 the most realistic predictions.

The limits to optimality are a priori *unknown* and can only be assessed empirically. Recent EEO approaches to photosynthetic optimality have made pragmatic choices 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 treated as constants. These assumptions are supported by observations but only as an approximation; all 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 and, indeed, competitive success does not necessarily require the optimum state to be achieved. 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. Again, empirical tests are important to determine whether the timescales of acclimation adopted for modelling purposes are realistic.

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. Although we do not review attempts to do so here, we note that an important test of existing approaches is whether 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 timescales 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).

Fire and land use. Wildfire is a major cause of vegetation disturbance and many models now explicitly stimulate the two-way interaction of wildfire regimes with vegetation and climate. However, the performance of these models is relatively poor beyond the largest-scale geographic patterns (Forkel et al., 2019; Hantson et al., 2020). This raises the issue of whether there is scope for EEO concepts to inform research and ultimately improve fire-vegetation models. Plants have, for example, evolved specific adaptations to different frequencies and intensities of fire (Clarke et al., 2013; Pausas et al., 2016; Pausas, 2019). Exploring the trade-off between the maintenance cost of these traits and fire frequency could lead to more mechanistic representations of vegetation-fire interactions in models and the ability to project the consequences of environmental changes in fire-prone regions better.

The impact of changes in land use on the biophysical properties of the land surface and on biogeochemical cycling has led to considerable attention being given to developing data sets to impose land-use history on vegetation models (e.g. Pongratz et al., 2008; Klein Goldewijk et al., 2017) and scenarios for future changes in the land biosphere under direct human intervention (including agriculture, pastoralism and forestry). Several vegetation models now explicitly simulate agricultural PFTs in order to be able to assess the likely impact of future climate changes on production and the human resource base. Arable crops represent an extreme modification of the landscape yet, within the constraints that have been imposed by artificial selection, crop growth conforms to the same principles as all plants and can be modelled with the same EEO-based tools (Qiao et al., 2020). Further work to explore the EEO approaches to anthropogenic land use would be useful, both from the perspective of providing more realistic or more parsimonious crop models and to harmonise modelling approaches for simulating the land biosphere within Earth System models.

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 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 (Heck et al., 2018). However, more reliable models are required to enhance confidence in the plausibility of many of these projections. The rate 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 by substantially reducing the number of parameters required that must be specified. As models move away from PFTs to explicitly representing plant traits, EEO approaches will make it possible to reduce the dimensionality of the trait-space that needs to be considered. The application of EEO 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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Box 1: How surface land 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 quantitative 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. Although there have been efforts to use available trait databases for defining PFT-specific parameterisations (e.g. Harper et al., 2016), models are still 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.

1195

Box 2: Steps towards a parsimonious model for gross primary production

We summarize here how EEO hypotheses were derived and tested and used to create a parsimonious model for GPP. For clarity, we describe a simplified model that assumes J_{max} is large. H. Wang et al. (2017) provide the full derivation.

(1) According to the FvCB model, photosynthesis proceeds at the lesser of two rates: A_C, determined by V_{cmax}, and $A_{J,}$ by light (with a maximum value determined by J_{max}). The coordination hypothesis (Field and Mooney, 1986; Chen et al., 1993; Maire et al., 2012; Quebbeman and Ramirez, 2016; H. Wang et al., 2017) states that these rates should converge. This is optimal in the sense that resources would be wasted if overcapacity were maintained in one process or the other. Thus, the hypothesis predicts that $A_C \approx A_J$ on the time scale of physiological acclimation. This time scale, from empirical studies, is on the order of a few weeks. Assuming (as a simplification) that the response of A_J to light is linear over the relevant range, then from the FvCB model if $A_C = A_J$ then

$$V_{\mathrm{cmax}}\,(c_i - \Gamma^*)/(c_i + K) \;=\; \varphi_0\, I_{\mathrm{abs}}\,(c_i - \Gamma^*)/(c_i + 2\Gamma^*) \qquad (1)$$

where c_i is the leaf-internal partial pressure of CO_2, φ_0 is the intrinsic quantum efficiency of photosynthesis, and Γ^* and K are parameters (the photorespiratory compensation point and the effective Michaelis-Menten coefficient of Rubisco, respectively) whose values, and dependencies on temperature and atmospheric pressure, are well-established and relatively invariant across all C_3 plants (as also assumed by all global models that rely on the FvCB formulation of photosynthesis). Acclimation of V_{cmax} then ensures that photosynthesis follows the right-hand equation.

(2) We still need to know c_i. This depends only partly on the ambient CO_2 (c_a). The least-cost hypothesis is a conjecture by Wright et al. (2013) that the combined costs (per unit photosynthesis) of maintaining water transport and carbon uptake capacities are minimized – as carbon uptake requires water loss, and therefore transport. Prentice et al. (2014) reformulated this criterion based on the FvCB model, and proved that there is a value of the ratio $c_i{:}c_a$ (denoted χ) that minimizes it. (See Dewar et al., 2018 for extensions and alternatives.) The costs of water loss capacity were assumed proportional to transpiration, and the costs of carbon uptake capacity to V_{cmax}. To minimize their sum, their derivatives must add up to zero:

$$a\,\partial\,(E/A)\,/\,\partial\chi \;+ b\,\partial\,(V_{\mathrm{cmax}}/A)\,/\,\partial\chi \;= 0 \qquad (2)$$

where A is photosynthesis, E is transpiration, and a and b are (as yet) unknown quantities. V_{cmax}/A can be derived from the FvCB model. E/A can be derived from the diffusion equation (for CO_2 entering and water exiting the leaf, both controlled by stomatal conductance): $A \;=\; g_s\, c_a\,(1 - \chi)$ and $E \;=\; 1.6\, g_s\, D$, hence:

$$E/A \;=\; 1.6\, D/[c_a\,(1 - \chi)] \qquad (3)$$

where g_s is stomatal conductance (to CO_2; conductance to water is 1.6 times larger) and D is the leaf-to-air vapour pressure deficit. The solution to equation (2) is:

$$\chi \;=\; \Gamma^*/c_a + (1 - \Gamma^*/c_a)\,\xi\,/\,(\xi + \surd D) \qquad (4a)$$

with

$$\xi \;= \surd\{b\,(K + \Gamma^*)/1.6\,a\} \qquad (4b)$$

Equation (4) allows us to derive c_i, which can be plugged into the right-hand side of equation (1).

(3) But what is the ratio b/a? In principle a should decline with increasing temperature, as water becomes less viscous. So this ratio can be written β/η^*, where β is a parameter and η^* is the (known) viscosity of water relative to its value at 25˚C. H. Wang et al. (2017) used global leaf stable carbon isotope data (a proxy for χ) to estimate a single, universal value for β by multiple regression. This is an approximation, of course, but H. Wang et al. (2017) could successfully predict the broad global patterns of χ; how it varies with temperature, vapour pressure deficit and elevation; and how it varies among plant types, purely as a consequence of their growing in different environments.

(4) Equation (1) predicts leaf-level photosynthesis. However, making the further assumption that the canopy behaves as a "big leaf", H. Wang et al. (2017) and Stocker et al. (2020) showed that the same equation could be used to predict GPP – provided the satellite-observed fractional absorbed photosynthetically active radiation (fAPAR) is used in the determination of I_{abs}. The model is an LUE model: i.e. GPP is proportional to I_{abs}. But now it is linked explicitly to the FvCB model. All of its parameters are independently known, or (like β) can be estimated from data independent of GPP. The full implementation (considering finite J_{max}) requires one more parameter; but this, too, can be estimated from independent data (measurements of the ratio of J_{max} to V_{cmax}).

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 (see Supplementary Information for further details). 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) (W14) and Smith et al. (2019) (S19). 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 represent the uncertainty in GPP calculated using the daytime partitioning method in the FLUXNET2015 dataset (Pastorello et al., 2020). Modelled and observed GPP are in units of μmol CO_2 m^{-2} s^{-1}. Figure redrawn based on analyses in Mengoli et al. (2021).

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 (H. 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 redrawn from analyses presented in H. Wang et al. (2020).

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. Figure redrawn from data and model results described in Lavergne et al. (2020a).

Figure 5. Observed (a) photosynthesis and (b) isoprene emission 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. The figure is redrawn from Morfopoulis (2014) and the model is described in Morfopoulis et al. (2014).

Figure 6. 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. All values are shown on a log scale. Data from evergreen species in the GLOPNET trait database (Wright et al., 2004). Figure redrawn from analyses presented in H. Wang et al. (2021).

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. Figure redrawn from data and model results described in Franklin et al. (2009).

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, see Supplementary Information for further details). 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) (W14) and Smith et al. (2019) (S19). 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.

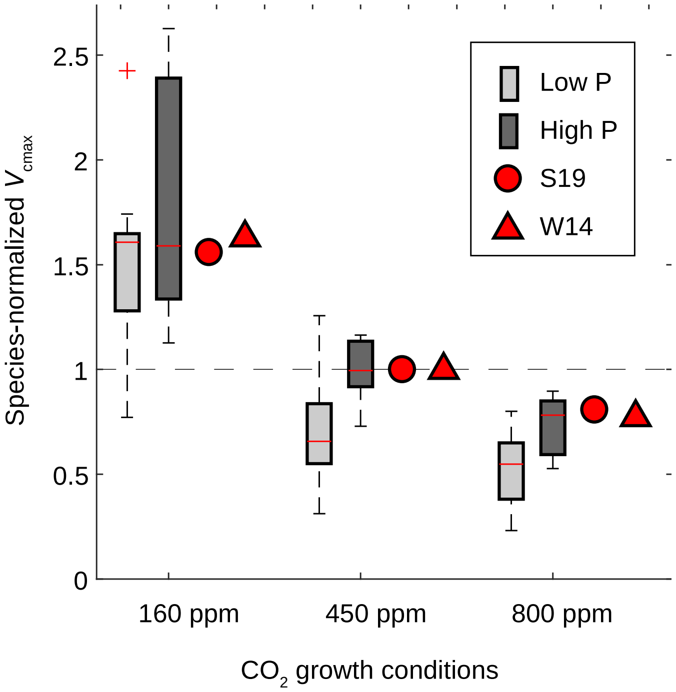


Figure 2. Observed (by eddy covariance, grey) and modelled (using the same parameter set, red) half-hourly gross primary production (GPP) during one week in August 2014 at sites in a tropical (GF-Guy) and a boreal (FI-Hyy) forest. Grey bands represent the uncertainty in GPP calculated using the daytime partitioning method in the FLUXNET2015 dataset (Pastorello et al., 2020). Modelled and observed GPP are in units of μmol CO_2 m^{-2} s^{-1}. Figure redrawn based on analyses in Mengoli et al. (2021).

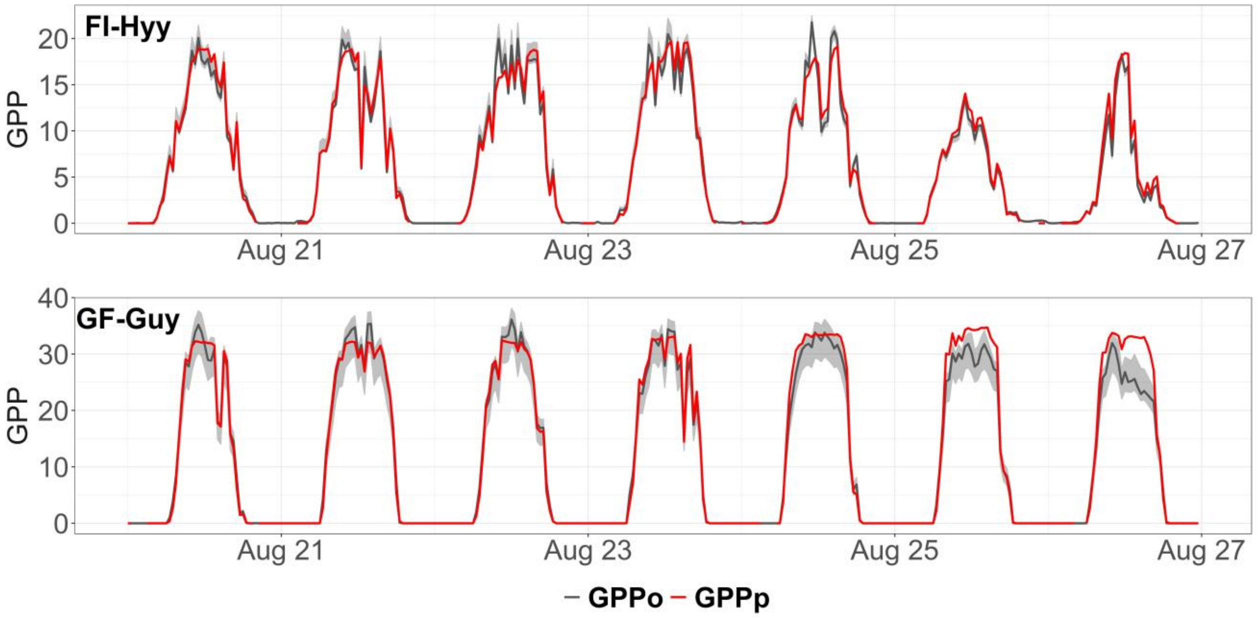


Figure 3. Field-measured (black lines) (a) leaf dark respiration rates (R_{dark}) and (b) photosynthetic capacities (V_{cmax}) compared to their modelled responses to growing-season temperature (red solid lines) as predicted by the coordination hypothesis (H. Wang et al., 2020). Both R_{dark} and V_{cmax} 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 redrawn from analyses presented in H. Wang et al. (2020).

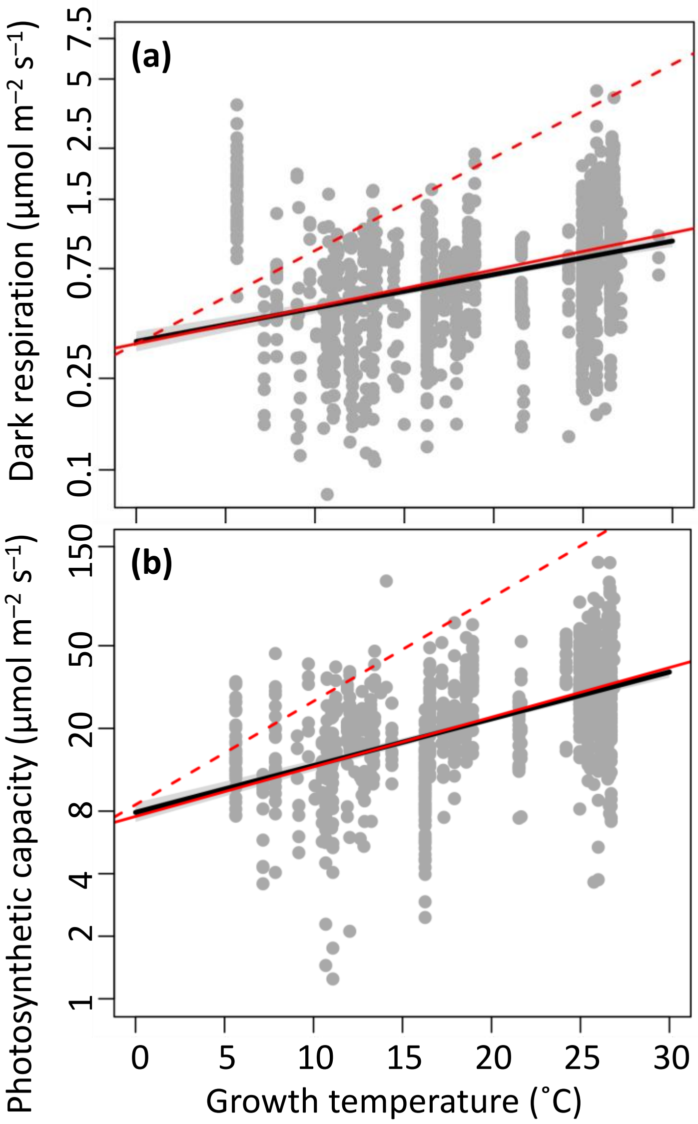
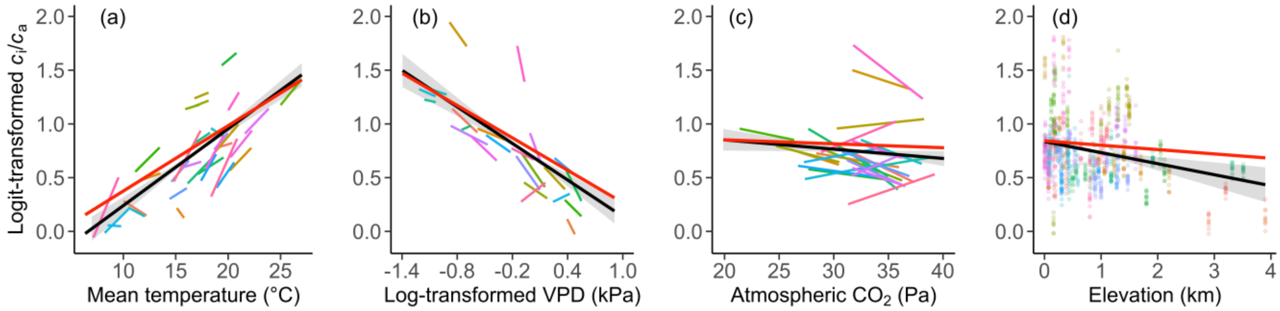


Figure 4. Trends in the ratio of leaf-internal to ambient CO_2 reconstructed from stable carbon isotope ratios in tree rings for different sites (coloured lines) and for the whole dataset (black) with respect to (a) mean growth temperature, (b) vapour pressure deficit (VPD), (c) atmospheric CO_2 and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



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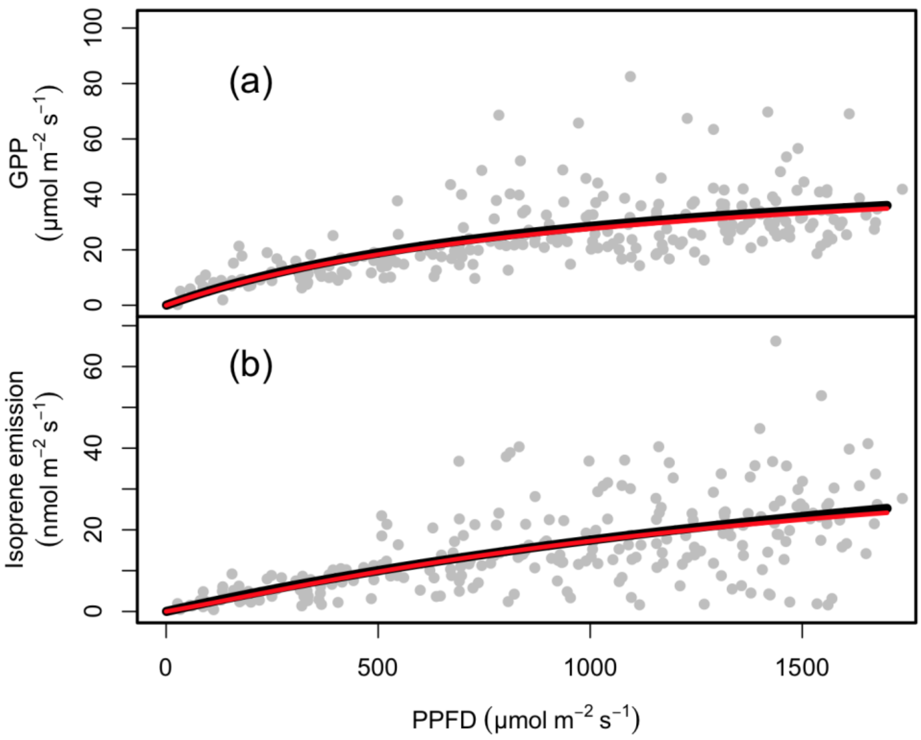

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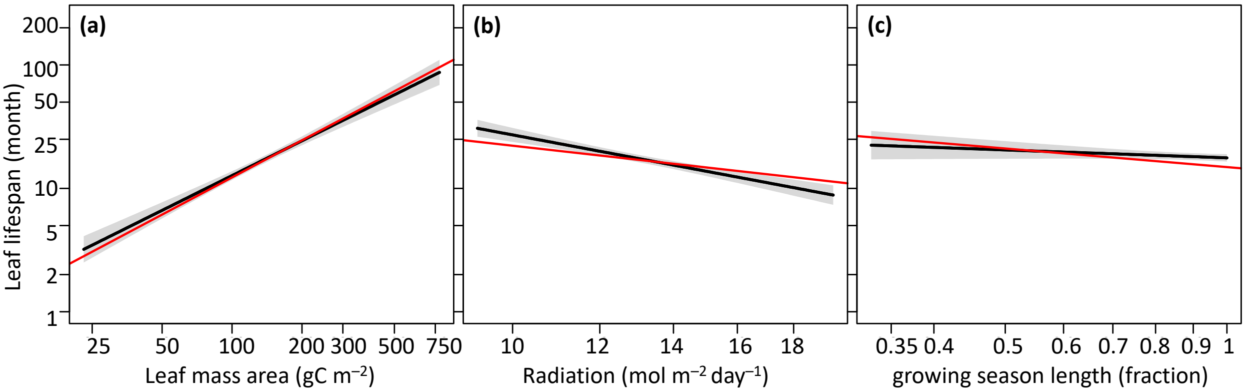

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