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Organizing principles for vegetation dynamics

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Abstract

Understanding vegetation dynamics is very challenging because of the multitude of contributing processes at widely different spatial and temporal scales. In this Perspective we propose that understanding of vegetation dynamics can be improved, permitting better predictions, based on organizing principles that constrain plant and ecosystem behaviour: natural selection, self-organization, and entropy maximization. Although these ideas are increasingly used, a limited common understanding of their theoretical basis has prevented their full potential to be realized. We explain the power of natural selection-based optimality to predict photosynthesis and carbon allocation responses to multiple environmental drivers, and how individual plasticity leads to the predictable self-organization of forest canopies. We show how models of natural selection acting on a few key traits can generate realistic plant communities, and how entropy maximization can distinguish between stochastic and deterministic drivers of vegetation patterns. We present directions for how these principles can be combined to improve the capacity of vegetation models to explain and predict the complex responses to environmental changes, resting on strengthened theoretical foundations.

Introduction – the challenge of vegetation complexity

Vegetation dynamics involves processes operating at widely different spatial and temporal scales, from stomatal opening and closing (minutes to days, at leaf level) to biome shifts (decades to centuries, across entire continents). Tremendous research efforts have been devoted to understanding and predicting how plant processes and functional traits at the level of individuals combine to determine the structure, function and dynamics of vegetation on larger scales. Because no single scientific discipline or theory deals with all processes, dynamic vegetation models (DVMs) have been developed that combine elements from several areas of research on plants and ecosystems – plant biogeography, biogeochemistry, plant physiology, forest ecology and micrometeorology. The most well-known DVMs, dynamic global vegetation models (DGVMs), have found a wide field of application including: assessments of land-atmosphere carbon, water and trace gas exchanges; water resources; impacts of environmental change on plants and ecosystems; land management; and feedbacks from vegetation changes to regional and global climates (Prentice and Cowling 2013, Fisher et al. 2014). DVMs have also been applied on local scales for testing of ecological hypotheses, and to practical questions in forest management and agriculture. All DVMs have in common that they are mechanistic, i.e. based on the assumption of universally valid mechanisms (processes), which may enable them to make predictions under conditions outside the range of observations.

Over time, DVMs became more complex as their developers strove to represent an ever-greater number of processes. However, this additional complexity has rendered models dependent on the provision of values of an ever-increasing number of parameters, many of which are poorly constrained by observations. This tendency has created a “complexity trap”, whereby apparent increases in realism are offset by decreases in transparency, robustness and predictive power (Prentice et al. 2015). In the last decade some important limitations of current DVMs have become apparent through strongly diverging predictions of C fluxes and vegetation cover among state-of-the-art DGVMs that have stubbornly resisted resolution (Prentice et al. 2015, Whitley et al. 2017, Pugh et al. 2018). Underlying reasons for these divergences include contrasting representations of N uptake, water responses, and mortality (Walker et al. 2015, Huang et al. 2016, Thurner et al. 2017). For example, DVMs have underestimated the ability of plants to enhance N uptake through increased below-ground C allocation and at the same time overestimate changes in leaf N (Medlyn et al. 2015),

resulting in overly strong projected nutrient limitations of future C sequestration (Sulman et al. 2019). C allocation is a key uncertainty in current DVMs (Montané et al. 2017, Xia et al. 2017) which is rooted in a lack of consensus as to how plants and vegetation acclimate to combined water, C and N resource variations.

Plant diversity is another key challenge. The effects of diversity have recently been evaluated in DVMs using observed plant trait variation as an input (Fyllas et al. 2014, Sakschewski et al. 2016) and some have even addressed the generation and dynamics of plant diversity in some ecosystems (Langan et al. 2017, Gaillard et al. 2018). However, it remains a general challenge to predict how diversity is maintained and may change over time. Including diversity in DVMs without sufficient understanding of its mechanistic basis may further aggravate the complexity trap.

In summary, substantial progress has been made in understanding individual plant processes, which is used to continuously enhance existing DVMs. While this improves predictions of current vegetation, the remaining problem is to reliably predict dynamics in response to environmental changes. Among the wide range of empirical and technical challenges linked to this problem here we focus on a particular but fundamental aspect: controlling principles of the dynamics of plants and communities. We argue that general organizing principles – based on natural selection and optimality, self-organization, and entropy maximization – can facilitate the development of more reliable vegetation models. These ideas are not new but have been explored primarily in small-scale and theoretical studies, and some are already in use in some prognostic DVMs. However, their full potential for explaining vegetation dynamics has not yet been realized due to limited common understanding of these concepts among empiricists, theoreticians and applied modellers. Here we aim to clarify the theoretical basis, and the potential and limitations, of general organizing principles for improving our understanding and ability to predict vegetation dynamics.

The concept of organizing principles

An organizing principle determines or constrains how components of a system, such as different plants in an ecosystem or different organs of a plant, behave together. In mathematical terms, it is an additional equation added to a system of equations, which allows one or more previously unknown variables in the system to be determined, thus reducing the total uncertainty. Here we highlight three key principles that are valuable for understanding the complexity of organisms and ecosystems and, we argue, will help vegetation models to escape the complexity trap. The first is natural selection, operating primarily on individuals (genotypes) and their traits but also on community composition. The second is self-organization, whereby the interactions of system components (including individual plants) can lead to a predictable system structure. The third is entropy maximization, a statistical selection principle which expresses the aggregated outcome of a large number of underlying stochastic processes subject to a small number of system-level constraints.

Natural selection – the “missing law” for vegetation modelling

All persisting plant traits and behaviours must have passed the filter of natural selection. Acting on individuals of a species, natural selection eliminates unfit or uncompetitive traits and trait combinations rapidly and effectively. Natural selection is thus the reason why species do not possess arbitrary combinations of important traits. Acting on differences between species, natural selection is a driver of population and community dynamics. It generates strong relationships among traits, and correlations between traits and environment, that are not mandated by physical laws alone. Therefore – and despite the underlying complex interactions among organisms, communities, and ecosystems – *natural selection is a key source of predictability in biological systems*. This simple and powerful idea allows models to predict more and require less input information (fewer uncertain parameters), which ultimately can improve both their predictive power, and our scientific understanding of the patterns they describe. However, the operational application of natural selection-based concepts to vegetation modelling is non-trivial, for several reasons.

Eco-evolutionary optimality shapes individual plants

Given that the evolution of traits and community composition are subject to natural selection for increased fitness, the resulting trait combinations may be predictable as those maximising fitness. Optimality approaches based on this principle can be seen as a shortcut to predicting evolved traits and how they vary with

environmental conditions (i.e. functional biogeography and phenotypic plasticity), without explicitly simulating the underlying evolutionary dynamics (Optimality here refers to eco-evolutionary optimality of the plants and not the *method* of optimization used to estimate model parameters). Optimality does not necessarily imply that there is an overall control mechanism (e.g. hormones) but may also result from bottom up effects, such as optimal allocation resulting from local sink and source dynamics in each organ (Thornley 1998) or coordination of processes (Chen and Reynolds 1997). Regardless of the underlying mechanisms, optimality hypotheses address the outcome of these mechanisms.

Optimality approaches often make use of economic concepts (Bloom 1986), expressing the fitness proxy and the traits optimized in terms of costs and benefits in a common currency – usually carbon (C) (fig. 1, Supplementary table 1). A key advantage of the optimality approach is that the fitness function integrates the effect of all processes and does not have to be calibrated for different conditions or species. This makes it suited to address complex and highly variable plant properties, such as C allocation and the pressing question how plants will respond to continued increases in atmospheric CO_2 concentration in the presence of other resource limitations. Based on the optimality hypothesis that plants minimize the combined C costs of maintaining photosynthetic capacity and supporting water transport, a photosynthesis model explains a large fraction of the global variation among biomes in leaf CO_2 uptake properties in response to multiple environmental factors using only two parameters that are common to all C_3 plants (Wang et al. 2017, Bloomfield et al. 2019) (Fig. 2). An optimality hypothesis stating that trees maximize net biomass increment and reproduction explains the interacting effects of elevated CO_2 and nitrogen (N) availability on tree growth and allocation, as observed in Free Air Carbon Dioxide Enrichment (FACE) experiments (Franklin 2007, Franklin et al. 2009) (Fig. 1). Maximization of a related fitness proxy also explained water use responses to elevated CO_2 in FACE experiments (Schymanski et al. 2015).

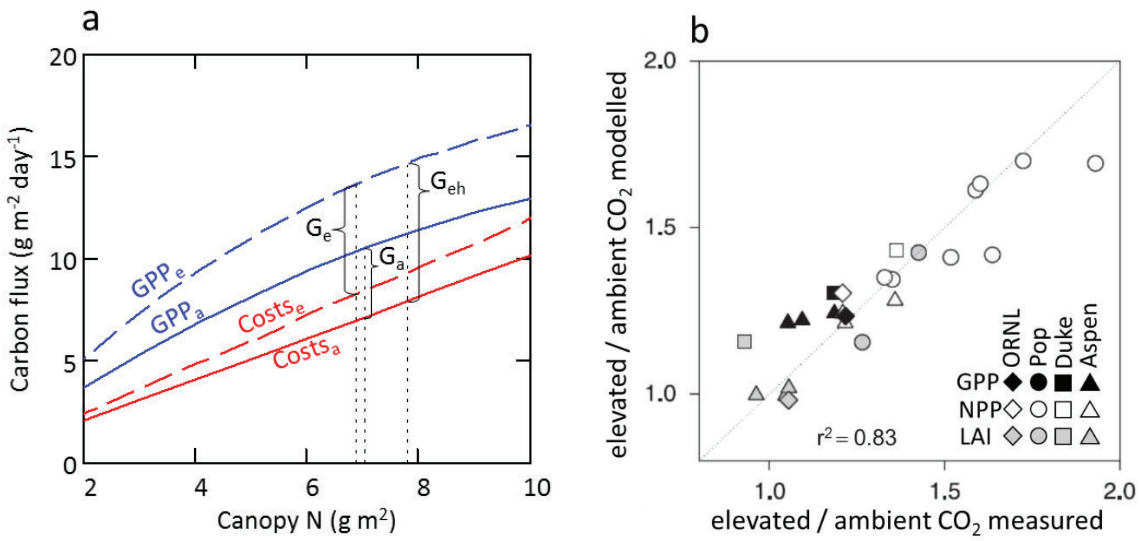

Figure 1. Optimality model of CO_2 and N availability effects in free air CO_2 enrichment (FACE) experiments. (**a**) The hypothesis is that trees optimize canopy N (vertical dotted lines) by maximizing net C gain, G = GPP – Costs, where costs are carbon costs for maintaining the canopy (respiration + leaf and root turnover). Elevated CO_2 increases GPP (subscript e) compared to ambient CO_2 (subscript a), causing a potential large increase in optimal canopy N and net C gain (G_{eh}), which is not realized due to a simultaneous increase in C costs per N uptake (due to soil N limitation), resulting in smaller net effect (G_e). (**b**) Modelled versus measured CO_2 effects on productivity (GPP and NPP) and leaf area index (LAI) in forest FACE experiments with sweetgum (ORNL), loblolly pine (Duke), poplar (Pop), and aspen. Adapted from (Franklin 2007) and (Franklin et al. 2009).

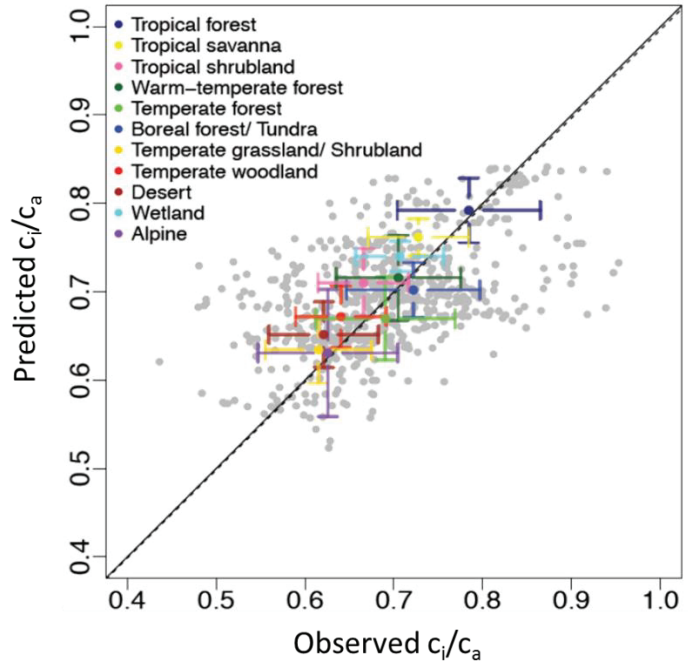

Figure 2. CO_2 uptake parameters predicted by optimality principle. Using uniform parameters in conjunction with a cost-minimizing optimality hypothesis, a theoretical model predicts the ratio of leaf-internal to ambient CO_2 (c_i/c_a) – a key index of leaf-level C and water exchange – across the world's biomes (Wang et al. 2017). The inputs are growing-season temperature, vapour pressure deficit and elevation. Observations (based on leaf $\delta^{13}C$ data) are compared with model predictions. Means and standard deviations are indicated for each biome, showing that although there is considerable unexplained variation among individual plants (grey points, r^2=0.26), biome means are well predicted by the model (r^2=0.73). The continuous line is the regression line (constrained through the origin); the dashed line is the 1:1 line.

Despite the power of eco-evolutionary optimality approaches to explain a wide range of observed phenomena (Supplementary table 1), only a few have been applied in prognostic DVMs (e.g. DGVMs), notably optimal stomatal conductance (De Kauwe et al. 2015, Xu et al. 2016, Eller et al. 2018, Kennedy et al. 2019) and also optimal leaf level N allocation (Xu et al. 2012). Optimal C allocation has also been addressed in a prognostic DVM, however not in terms of optimal acclimation (as in Fig. 1) but as an outcome of competition between different plant types, each with a fixed allocation (Weng et al. 2015). It is not straight forward to introduce optimal allocation in existing DGVMs because it requires a rethinking of the structure, from a typically sequential C flux from one compartment to the next to an inter-linked regulation of leaves, stem, and roots based on the costs and benefits of all limiting resources. However, in addition to this real technical challenge some conceptual confusion may have hampered the application of optimality in prognostic DVMs.

A potential argument against the optimality approach is that in a variable and fluctuating environment optimality may never be reached (Fisher et al. 2015). This however rather calls for a careful analysis of the appropriate temporal and spatial scale of the fitness proxies and the environmental variables and vegetation responses analysed (Schymanski et al. 2015). At the leaf scale, the cost efficiency of leaf photosynthesis in terms of water and C use has been used as a fitness proxy to predict regulation of stomatal conductance (Medlyn et al. 2011, Manzoni et al. 2013, Dewar et al. 2018). At the whole plant scale, maximization of fitness proxies related to whole plant production has been used to predict CO_2 uptake, root distributions (Schymanski et al. 2009, Guswa 2010, Yang et al. 2016), C allocation (Franklin et al. 2012), and tree height (King 1990). By also including survival in the fitness proxy, an optimality model explained broad patterns in such whole-life dependent strategies and traits, such as observed spectra of growth rate, mortality, wood density, and drought response in trees (Franklin et al. 2014b). Hypothetically, and in contrast to previous attempts to separate ontogeny and “true” plasticity (McConnaughay and Coleman 1999), a whole plant fitness proxy could also be used to model ontogeny of traits as a form of plasticity, based on the effects of increasing size on fitness costs and benefits.

Another source of confusion is a perceived conflict between optimality and the evolutionary stable strategy (ESS, the strategy, or trait values, emerging from competition among alternative strategies) (Hikosaka and Anten 2012, Fisher et al. 2015). Based on game theory, it may be argued that evolution does not result in optimal solutions, because the winning strategy in competition with others (the ESS) is not the same as the optimal strategy in the absence of competitors. However, the conflict disappears once it is recognized that, (i) optimality is defined at the individual level, and (ii) if competition plays a role for the trait in question, then its impact has to be included in the definition of the environment, which otherwise would be incompletely defined. Effects of competition can be included in the fitness proxy, e.g. by maximizing height growth as the winning strategy under competition for light (Valentine and Mäkelä 2012), or by explicitly modelling the competition for light and nutrients (King 1990, Franklin et al. 2012), water (Farrior et al. 2013), or mycorrhizal N supply (Franklin et al. 2014a). Competition can have large effects on optimal behaviour. For example, competition for water reduces the benefits of saving water and leads to different optimal stomatal behaviour than non-competitive optimality (Wolf et al. 2016).

An important – yet still largely ignored – question is to what extent trait variation along environmental gradients is due to phenotypic plasticity (individual acclimation) or genotypic differentiation. Traits differ in this respect (Meng et al. 2015, Dong et al. 2017, Yang et al. 2018) and the difference is critical for the time scale of changes, as plastic acclimation of traits is fast compared to mean-trait changes due to shifts in community composition. Further, although often clumped together in empirical studies, plasticity is not equivalent to intraspecific variation, because the latter may also include non-plastic variation. While plastic traits acclimate to the current environment, non-plastic variation has been shaped by the whole evolutionary history, which is significantly more challenging to represent and makes it precarious to predict non-plastic traits from the plant’s current environment. However, some inter-relationships between different traits (rather than trait versus environment) may be more predictable across variable environments, as indicated by trait economics spectra (Wright et al. 2004, Reich 2014, Díaz et al. 2016). These relationships can not only be used to reduce the number of independent traits (degrees of freedom) in models, but also to test optimality hypotheses, which can explain the mechanisms underlying the trait relationships (McMurtrie and Dewar 2011, Maire et al. 2013) – and thus be used to predict how the trait relationships may vary across environments, in time as well as in space.

Fitness-based optimality is well-defined only at individual or genotype level and predict a single strategy or plant type for a given environment. However, although real communities usually consist of many coexisting types, the single optimal strategy may be a good first-order approximation of the dominant plant type in a given environment. For example, a model that postulates that plants optimize the proportions of leaf, stem and root growth to compete with neighbours for N and C (resulting in an ESS) successfully reproduces observed global distributions of primary production and the allocation of N and C to leaves, stems and roots (McNickle et al. 2016). This finding suggests that maximization of individual competitiveness for resources, is a useful optimality principle to explain the dominant vegetation type and traits in a given environment. Moreover, it may be possible to use an optimality approach to address diversity by generating a range of equally or similarly optimal strategies (Marks 2007). A key advantage of the optimality compared to alternative empirical community-mean-traits approaches, e.g. (van Bodegom et al. 2014), is that the fitness function integrates and thereby accounts for covariation among traits (Laughlin and Messier 2015, Clark 2016).

In summary, the theory of eco-evolutionary optimality is a powerful approach to predict plant traits as a function of environmental conditions, especially for plastic phenomena such as C and N allocation, which is a weak spot in predictive DVMs (Achat et al. 2016). There is also a considerable potential to use optimality hypotheses to better understand how and why different plant traits co-vary, and to apply them in both DVMs and empirically based frameworks to improve predictions of how traits and species distributions respond to environmental changes.

Emerging communities and functional diversity

Optimality concepts help in predicting a single (or dominant) strategy or plant type in a given environment, but they do not predict biodiversity within a site (α-diversity). For understanding vegetation dynamics, functional diversity – variation in functional traits among the plants in a community – is the most relevant aspect of biodiversity (Tilman et al. 1997). Natural selection drives the evolution of traits and community dynamics precisely by operating on functional diversity; so the concept is fundamental for understanding community dynamics in the long term. The inability of many current DVMs to realistically account for functional diversity has been shown to cause underestimation of local acclimation and adaption (de Almeida Castanho et al. 2016), artificial threshold behaviour (Kleidon et al. 2007, Lavorel et al. 2007), and underestimation of the resilience of vegetation to environmental change (Sakschewski et al. 2016). Functional trait diversity has been included as an input in a tropical forest model to improve its predictions of ecosystem processes (Fyllas et al. 2014, Sakschewski et al. 2016). This approach however does not address the generation and maintenance of diversity over time. Diversity-generating approaches were pioneered in a simulation of the large-scale biogeography of marine phytoplankton (Follows et al. 2007) and have been applied to theoretical analysis of vegetation dynamics (Scheiter et al. 2013, Falster et al. 2017) and even to the prognostic modeling of tropical ecosystems (aDGVM2 (Langan et al. 2017, Gaillard et al. 2018)). How best to represent functional diversity in DVMs nonetheless remains an open question.

Functional diversity can be viewed as the outcome of two interacting effects: environmental filtering by the abiotic environment determines where a plant can potentially survive (the fundamental niche), while biotic interactions determine which plants can persist together (the realized niche). Environmental filtering is relatively straightforward to model (Pavlick et al. 2013) but coexistence is much more difficult. One approach is to more-or-less explicitly model the process of natural selection to derive trait combinations (genotypes or species) corresponding to evolutionary stable strategies (ESS), i.e. an ESS-community that cannot be invaded by other strategies (Hofbauer and Sigmund 1988, Falster et al. 2017). By embedding the process of natural selection within models, functional diversity becomes an emergent property of ecosystems, thereby avoiding the need to pre-specify trait combinations or the number of types or species within a model. This approach may also provide a framework for addressing evolutionary adaptation to a changing climate (Jump and Peñuelas 2005, Franks et al. 2007).

The community ESS concept provides a way to generate and test hypotheses on co-existence (mechanisms that prevent one species from out-competing another) that can be applied in predictive models. In such a model, successional processes involving size-structured competition for light and disturbance can maintain functional diversity in a plant community (Falster et al. 2017). By allowing species to differentiate along two functional trade-offs, functional diversity could be recovered despite the absence of any imposed

environmental heterogeneity (Fig. 3). However, without disturbance and the process of growing from seed, diversity in this model disappears. It follows that successional processes and individual dynamics need to be included in order to maintain diversity in vegetation models; processes that are represented in recent demography-enabled DVMs (Medvigy et al. 2009, Weng et al. 2015, Fisher et al. 2018), which therefore possibly could be further developed into diversity-enabled prognostic DVMs.

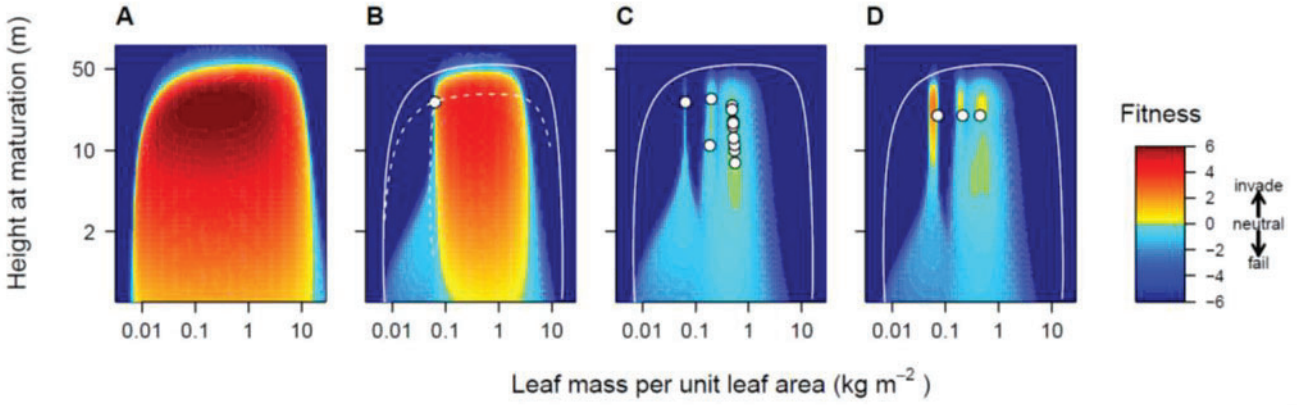

Figure 3. Modelling diverse communities based on evolutionary stable strategies. By modelling reproductive success in competition with existing types (white dots), ESS models estimate the fitness of potential invaders (coloured shading) and use this to guide community assembly. Here species are allowed to vary in two traits, underpinned by physiological trade-offs. A) Initially, a wide variety of trait combinations have positive fitness and could establish. B) Through directional selection, any single species is driven towards a local evolutionary attractor. However, this single species cannot prevent the invasion of other types, if regions of positive fitness occur elsewhere in trait space. C) Through repeated rounds of mutation and selection, an ESS mix may be established, i.e. existing residents all have positive abundance while fitness is zero or negative elsewhere. The ESS trait mixture represents a prediction for the system diversity. D) In traditional models with pre-specified trait combinations, species may coexist, but are not evolutionarily stable – i.e. they could be invaded if new plant types were allowed into the system. In each panel, the solid white line delimits trait combinations that are not viable even in the absence of any competition (pure environmental filtering, as indicated in Panel A). In panel B, the dashed white line shows the evolutionary attractors for each trait when allowed to evolve in isolation (Falster et al. 2017).

However, while the diversity-enabled models are advancing the science of vegetation dynamics, developing them into prognostic tools pose additional challenges compared to traditional DVMs, such as the testing and calibration of diversity maintaining mechanisms. In particular, the predictive ability of diversity-enabled models is potentially limited by the set of traits and coexistence mechanisms that are accounted for. In addition to trade-offs between costs and benefits of traits linked to resource (light) competition discussed above (Falster et al. 2017) there are many mechanisms of coexistence, involving resources, natural enemies, spatial heterogeneity, and temporal variability (Loreau 2010, Adler et al. 2013), making species coexistence a high-dimensional problem (Clark et al. 2007). For example, complementarity – more species can use the total resources more completely – has been shown to reduce competition and promote coexistence in theoretical and empirical studies (Loreau 2010, Cardinale et al. 2012, Craven et al. 2018, Isbell et al. 2018) and therefore deserves more attention in future applied DVMs. While explaining the basis and roles of biodiversity has long been at the centre of interest among theoretical and empirical ecologists (García-Palacios et al. 2018), it is now also becoming critical for DVMs.

Self-organization at the ecosystem level

While plant processes and behaviours originate at the level of individuals that are subject to natural selection and environmental constraints, the collective actions of individuals also drive patterns and processes that can provide organizing principles at the ecosystem level. For example, the collective spatial behaviour of plants gives rise to remarkable patterns in vegetation structure that provide both scientific insights, and possible ways to reduce model complexity.

Self-organization simplifies forest structure

In forests, the individual acclimation (plasticity) of stem angles, leading to the collective organization of crown layers, is an example of self-organization at the ecosystem level. The most computationally intensive aspect of many forest dynamics models is the calculation of plant light availability based on all individuals' locations heights, and shapes (Moorcroft et al. 2001, Weiner et al. 2001). Despite their detail, however, these individual-based models often do not produce realistic-looking forest stands. There are too many gaps, and the emergent "jig-saw puzzle" canopy pattern is missing. The Perfect Plasticity Approximation (PPA) was developed to correct the problems of both computational intensity and unrealistic canopy. The PPA is based on the observation that individuals can move their crowns horizontally towards sunlight (phototropism), which leads to a simple pattern (Fig. 4): Canopy trees fill the horizontal space and there is approximately one height above which individual crowns are sunlit and below which individuals are in the shade of those canopy trees (Strigul et al. 2008). There will be a single height of canopy closure, and information on the locations of stems is no longer needed to calculate access to light. A rule defined at the level of individual trees (the search for sunlight) thus leads to a simple, emergent pattern that greatly simplifies the modelling of forest stand dynamics (Purves et al. 2008).

The PPA has also made possible the analytical ESS analysis of allocation strategies and predictions of their variation across environmental gradients in temperate forests (Dybzinski et al. 2011, Farrior et al. 2013, Farrior et al. 2015). Although many tropical forests exhibit a different size structure, the same individual rule of phototropism, though with different growth rates for canopy trees and frequency of stand-level disturbance, predicts the emergent structure of tropical stands (Farrior et al. 2016).

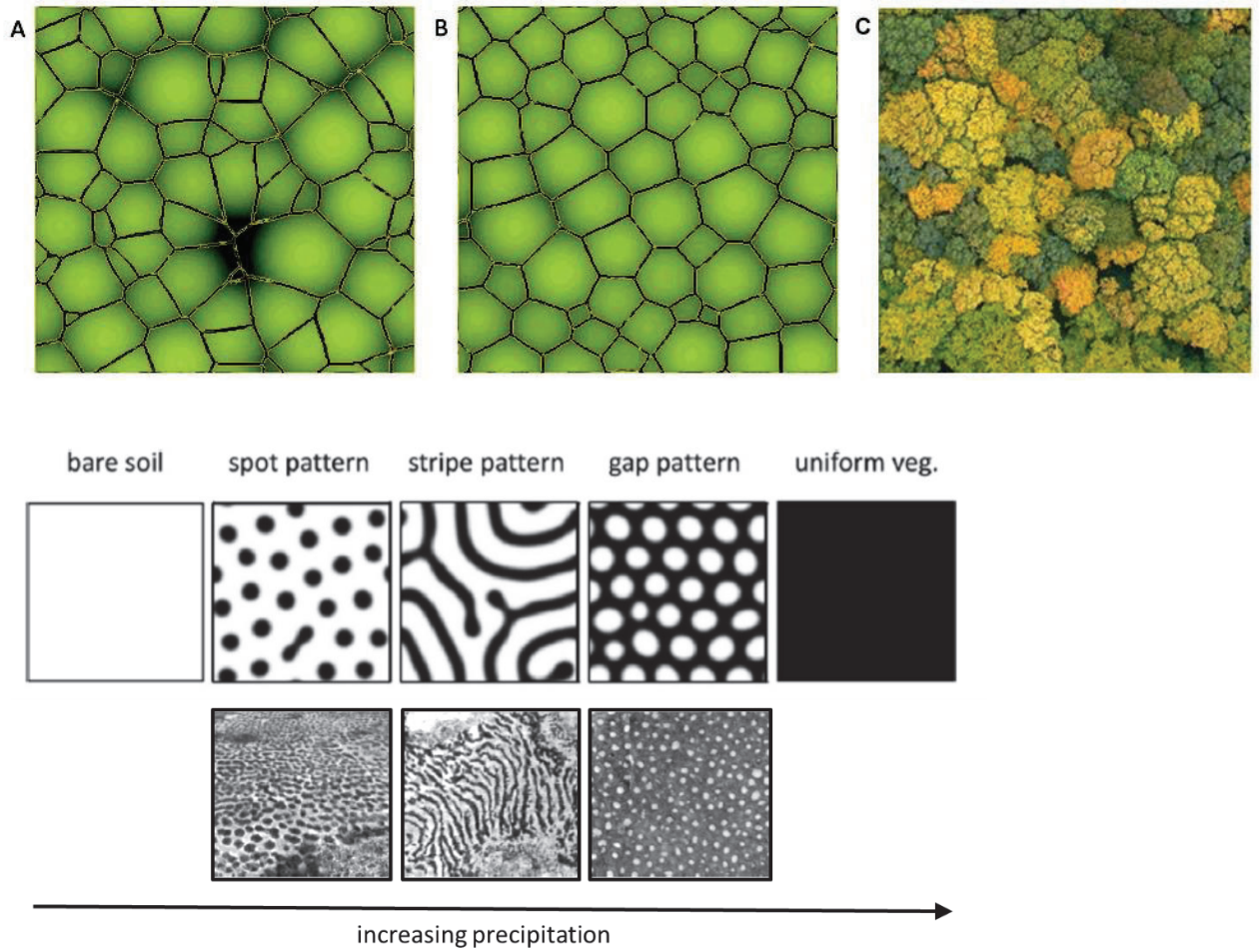

Figure 4. Spatial self-organization in ecosystems. A-C) Individual level phototropism leads to emergent regularity in forest crown height and size. Model and forest images from above. A) A forest dynamics model without phototropism (Strigul et al. 2008). B) The same forest dynamics model with individual phototropism (individuals allowed a maximum of 5° lean in their trunks). Brightness indicates the height of the canopy. Note with phototropism, canopy height and crown

size are more regular. C) Image of a near-natural forest in the Hainich National Park, Germany. A and B redrawn from (Strigul et al. 2008) Figure 7, and C from (Getzin et al. 2012) , Figure S1. D) Spatial self-organization in dry lands. Typical sequence of vegetation patterns along a rainfall gradient. Modeled (upper panels) and observed (lower panels), redrawn from (Meron 2016).

Spatial self-organization at the landscape scale

Spatial self-organization is driven by feedbacks between vegetation and the environment. For example, when trees establish in grasslands, they shade and suppress light-demanding grasses, competitively favoring other trees and eventually stabilizing patches of forests (Favier et al. 2004). Dryland landscapes provide another striking example of vegetation self-organization into regular spatial patterns (Fig. 4b) caused by positive feedbacks between local vegetation growth and water transport towards the growth location, by laterally extended roots, overland water flow, or soil-water diffusion (Meron 2012). That is, water transport helps vegetation growth, and that growth, in turn, enhances the water transport. The emergence of these patterns can be modeled in spatially continuous models, which reveal that the underlying positive feedback loop is a common organizing principle for spatial patterns across different locations and systems. The spatial self-reorganization in response to reduced rainfall slows desertification and results in successive state transitions to patterns of lower productivity (Fig. 4b), rather than in abrupt, direct collapse to bare soil (Rietkerk et al. 2004, Meron 2016). Vegetation patterning can also promote species coexistence and help mitigate biodiversity loss (Gilad et al. 2007, Meron 2016). However, the process is missing in general prognostic DVMs, perhaps due to the difficulty of representing spatial feedbacks in these spatially discrete (cell or gap-based) models. This problem may be addressed in future DVMs when enhanced computational power allows sufficiently high spatial resolution for explicit modeling of spatial feedbacks. Alternatively, the regularity of the patterns across rainfall gradients suggests that it may be possible to find universal approximations of their impacts, such as scaling relationships between fraction of vegetation cover and NPP or biomass (Glenn et al. 2008). Such a relationship could readily be incorporated in large-scale DGVMs or land-surface models to account for the larger scale impacts of fine scale spatial feedbacks without modeling these explicitly. The idea of simplification by upscaling, or aggregation is also central to another simplifying organizing principle, entropy maximization– as discussed next.

Entropy maximization – making order from chaos

Ecosystems are complex systems with myriads of interacting organisms and processes, yet there are obvious patterns in their macroscopic features. This fact echoes the situation in physics where, for example, reproducible relationships among the pressure, temperature and volume of a large assembly of molecules emerge from the chaos of the underlying molecular collisions. The principle of Maximum Entropy (MaxEnt (Jaynes 2003)) has proved successful in predicting those relationships from a statistical perspective, as the most likely outcome of the underlying microscopic variables treated as random noise within the imposed experimental constraints (e.g. fixed volume and temperature). MaxEnt can be applied at many scales but the most interesting from the point of view of vegetation dynamics is the ecosystem scale where the aggregated behaviour of large numbers of interacting individuals may to an extent be treated stochastically within the limits imposed by community-level environmental constraints (e.g. community resource use = resource availability). The stochasticity means that many ecosystem states (e.g. vegetation cover in a grid cell) can correspond to the same resource use (constraint) and MaxEnt predicts the probability of each state based on the number of ways it can be realized. Thus, in contrast to both purely mechanistic models and climate-based species distribution models MaxEnt does not *ignore* stochastic factors but *accounts* for their effects.

Identifying the stochastic and deterministic drivers of community assembly

MaxEnt is not a purely stochastic principle because the description of community resource use (e.g. of water or nitrogen) within the resource constraints requires some underlying biology to be modelled deterministically. MaxEnt enables us to test the assumed division between stochastic drivers (treated as random noise) and deterministic drivers, or mechanisms (treated as constraints): agreement between MaxEnt

predictions and observations indicates that the correct distinction has been identified; disagreement signals missing constraints or mechanisms. In MaxEnt, extension to more than one resource constraint is straightforward.

An illustrative example is the use of MaxEnt to predict statistical patterns of tree-grass distribution over large areas of tropical savannas across a gradient in water availability (Bertram and Dewar 2013). The key constraint was assumed to be the mean annual community-scale water balance (evapotranspiration = water availability), with a simple hierarchy in the water use of trees versus grasses versus bare ground. The broad agreement between predictions and satellite-based data (Fig. 5) suggests that, indeed, the main deterministic driver of global patterns in tree-grass distribution is mean annual water availability, and the essential biology that needs to be modelled deterministically is the higher water demand of trees compared to grasses and bare ground. Other processes, which include disturbances by fire and herbivory, contribute to the statistical spread of the data in Fig. 5 at any given water availability, and can be treated as random noise that has no systematic effect on the mean trends.

An important caveat here is that just as the laws of probability only predict the most likely frequency distribution of heads and tails in a long run of coin tosses, and not the outcome of an individual toss, MaxEnt only predicts the most likely frequency distribution of tree-grass cover fractions across many sites, and not the tree-grass cover fractions at a given site (an individual data point in Fig. 5). The latter would require explicit representation of, and site-specific information about, other processes such as fire history and herbivory.

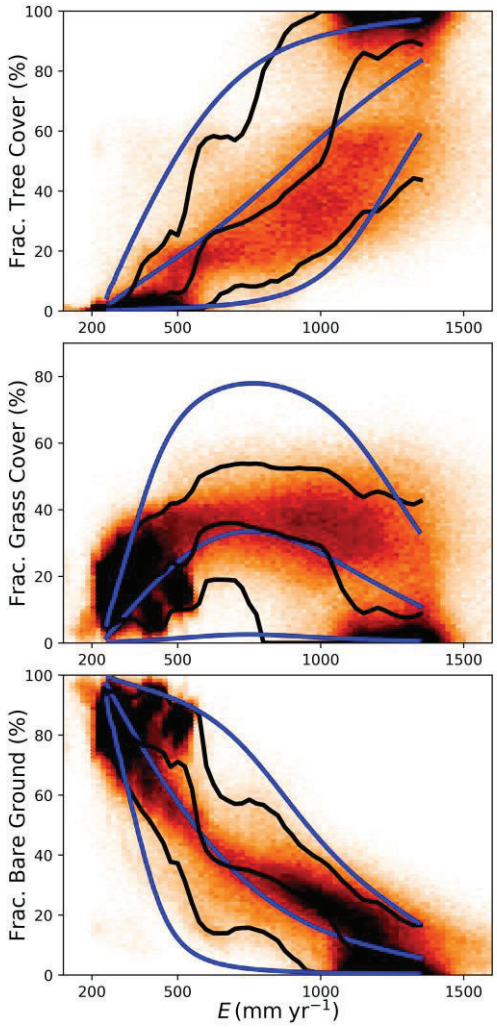

Figure 5. Vegetation distributions predicted by the principle of maximum entropy (MaxEnt). Observed and modelled frequency distributions of tree, grass and bare ground cover fractions vs. mean annual water availability (*E*) in tropical savannas at a 1 km^2 resolution. Points: frequency histogram of satellite-based (MODIS) fractional cover estimates

sampled from Africa, South America and Australia. Black curves (from bottom to top): 5th percentile, mean, and 95th percentile of the observed sample frequency histogram *vs. E*. Blue curves (from bottom to top): 5th percentile, mean, and 95th percentile of the modelled frequency distributions *vs. E*. Adapted from (Bertram and Dewar 2013).

In this simple example, the link between MaxEnt and the underlying biology occurs through the assumed water use rates e_i of each cover type *i* (trees, grass, bare ground), which determine the community water use that appears in the water balance constraint. MaxEnt then predicts that the cover type with the highest (lowest) value of e_i dominates at high (low) water availability (Fig. 5). A natural generalisation of this approach would be to replace assigned values of e_i by an eco-physiological optimality model, $e(\boldsymbol{FT}, \boldsymbol{FT_o})$, for the dependence of plant resource use on plastic acclimating traits ($\boldsymbol{FT_o}$) and other plant functional traits ($\boldsymbol{FT}$). Then, at high (low) resource availability MaxEnt would predict a relative abundance distribution in trait space that follows the peaks (troughs) of $e(\boldsymbol{FT}, \boldsymbol{FT_o})$, thus establishing a link between diversity in $\boldsymbol{FT}$ and $\boldsymbol{FT_o}$ at the community level and optimality at the individual level ($\boldsymbol{FT_o}$). Effects of climate change could also be incorporated through the additional dependence of *e* on environmental conditions.

MaxEnt based approaches could potentially be developed to incorporate stochastic effects on coexistence and in DVMs, and to identify the key deterministic drivers that generate and maintain diversity – an important challenge for understanding long-term vegetation dynamics, as discussed below.

A roadmap for the use of organizing principles in vegetation modeling

We have demonstrated the nature and utility of three types of organizing principles in explaining and predicting different aspects of vegetation dynamics. We propose that the principles can be combined in a hierarchically structured framework for vegetation modeling, from functional traits (FTs), to species (or plant functional types), to stand structure and community composition (Fig. 6). We do not attempt to provide a complete blueprint for the development of next-generation DVMs. Instead we highlight some fundamental challenges that the organizing principles can help address, with focus on dynamics at individual to community scales.

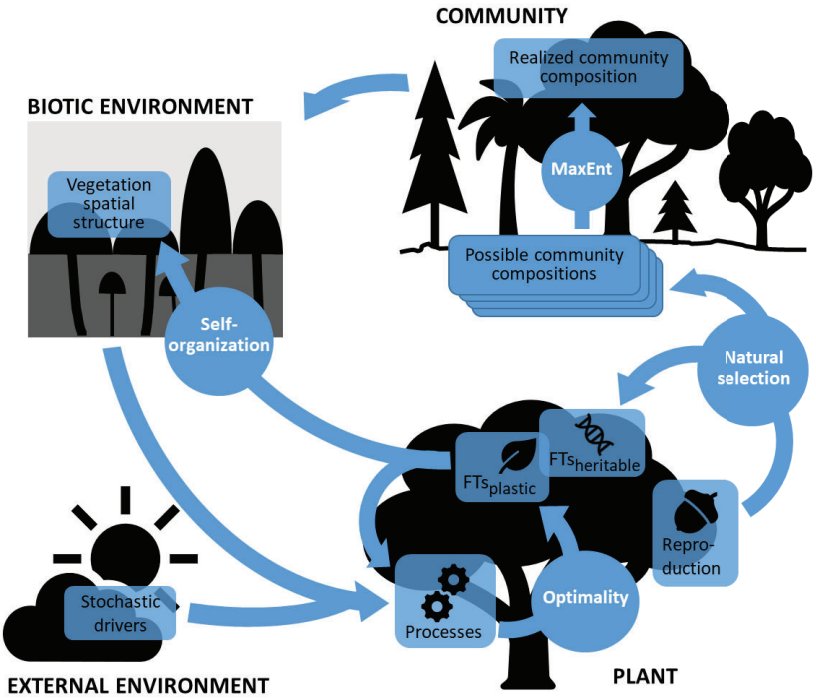

Figure 6. Framework for the use of organizing principles in vegetation modelling. Each organizing principle (circles, white text) helps predict (arrows) different vegetation properties (boxes). Natural selection drives the evolution of heritable functional traits (FTs). Phenotypic plasticity is predictable through fitness-proxy maximization (optimality). Collective self-organization among many plants results in predictable patterns of spatial structure at the stand level (e.g. due to plasticity of stems, the Perfect Plasticity Approximation -PPA). Natural selection controls community dynamics together with stochastic factors. Many different community compositions may be possible and the most likely may be predicted by

entropy maximization (MaxEnt). The external environment includes abiotic factors and all other external drivers such as disturbances.

Which functional traits are most relevant?

In DVMs, plant species (or functional types) are defined in terms of a number of FTs, for which measured values are available, and which have been observed to vary among plants and to be important for plant function. Our perspective implies more precise criteria for how to select and use FTs. First, the observation that only two underlying dimensions of variation explains 75% of the global variation in key FTs (Díaz et al. 2016) suggest a potential to reduce the number of FTs used to define species compared to most current DVMs. Furthermore, we propose a shift from the traditional approach of using measurements (e.g. mean values per PFT) of traits directly in models towards using traits measurements to test optimality principles and quantify interrelationships that constrain trait values (Fisher et al. 2015). Plastic traits which vary with environmental conditions, such as leaf:stem:root ratios, relative growth rate, and height, should not be used to define species. Instead they can be predicted based on optimality approaches (as described in the section on Eco-evolutionary optimality and Supplementary table 1). An efficient representation of species should be based on a few functionally important FTs that are as non-plastic (heritable) as possible (Fig. 6). To establish such FTs, observed trait variation and function can be analysed in new ways that separate plasticity from other sources of trait variation (Niinemets et al. 2015). For example, SLA is commonly used to define species in terms of a mean value although it varies strongly with environmental conditions, even within individuals (Scheepens et al. 2010). To resolve this problem, SLA could be separated into a non-plastic maximal SLA and a plastic component.

Once a set of non-plastic FTs have been identified, observed inter-relationships between them (trait spectrums) can be used in two ways: (i) to constrain potential species in terms of possible (or more or less probable) trait combinations to generate candidate species in model of community or (ii), they could be used to calibrate and evaluate ESS approaches such as (Falster et al. 2017)) which predict such inter-trait relationships.

How should vegetation structure and competition be modelled?

As discussed in section *Self-organization at the ecosystem level*, self-generating spatial structures have strong effects on vegetation dynamics by both generating and reducing heterogeneity. The latter effect is used in the PPA to simplify models of light competition in forest canopies, but the question is: can the PPA be applied for all forest or what are its limitations? Intuitively, PPA appears well suited to low diversity canopies whereas its binary light availability may lead to artificial exclusion of species with low shade tolerance in more diverse communities. Or could such problems be resolved by a sufficiently high spatial resolution in the critical canopy height? Similarly, while competition below ground can be readily modelled by assuming common pools of soil resources for all plants in a stand, the actual spatial extent of competition for nutrients and water is not well understood despite potentially large impacts on key processes, such as root growth (Farrior 2019) water use (Wolf et al. 2016) and whole plant growth (Franklin et al. 2012). Thus, although the representation of vegetation structure and competition has been improved in recent DGVMs (Weng et al. 2015, Fisher et al. 2018), quantitative evaluations of the accuracy and efficiency of different approximations of vegetation structure and competition are urgently needed.

How can we handle the complexity of communities?

As discussed in the section *Emerging communities and functional diversity,* DVMs have emerged recently that generate communities by modeling the natural selection process (diversity-enabled DVMs, (Scheiter et al. 2013, Falster et al. 2017)). While the prognostic use of these innovative approaches is yet limited (Langan et al. 2017, Gaillard et al. 2018), compared to traditional DGVMs they have a fundamentally improved capacity to predict long-term ecosystem dynamics under climate change. This includes biome shifts and the role of biodiversity for ecosystem resilience. Adding individual plasticity in addition to diversity in these models (as described above) could lead to novel insights in how plasticity and community dynamics interact and influence the rate of adaptation of vegetation to climate change, which is critical for projections of future vegetation

processes and carbon balance (Chevin et al. 2010, Walker et al. 2015). The need to model both individual plasticity and community dynamics further highlighted by the observation that they sometimes drive mean values for FTs in opposite directions along environmental gradients (Kichenin et al. 2013).

A critical question for the further development of community ESS approaches is if the relevant coexistence mechanisms are included. An important, but often neglected, factor in this context is demographic and environmental stochasticity. The MaxEnt approach has been used to account for randomness in predicting community composition, i.e. the abundance of each species, using mean trait values as site level constraints (Shipley et al. 2006). Potentially, a similar approach may also be applied with a (deterministic) diversity-enabled DVM that represents the hypothesized coexistence mechanisms and with resource availabilities as additional constraints. For given resource availabilities there is stochastic variation in environmental variables and plant demography (e.g. recruitment and mortality) and the DVM generates many communities with different species compositions. The mechanisms incorporated in the DVM and the resource availabilities influence the probability (or frequency) that a given community is generated. Based on the generated accumulated distribution of community compositions, MaxEnt is used to find the most likely community composition. The MaxEnt model's ability to explain observed community compositions is then a measure of the relevance of the hypothesized (deterministic) coexistence mechanisms, as described in the section "Identifying the stochastic and deterministic drivers of community assembly".

In conclusion, the principles and approaches put forward here all address the same underlying key challenge in the science of vegetation dynamics – how to make sense of complexity. During the initial development of DVMs (1980s), very few ecologists were looking for general patterns in nature. The phrase "despairing empiricism" (Prentice 1998) was coined to describe the view (still held in some circles) that such patterns do not exist – implying that models will always require large numbers of parameters to be measured directly, rather than predicted from underlying principles. Since then many promising but sometimes diverging approaches have emerged. With the perspectives on organizing principles presented here we hope to contribute to a coherent theoretical basis for explaining and predicting interactions among plants and the environment. While many other strands of vegetation research not discussed here are also needed for this, organizing principles are necessary for putting progress on different processes and traits into a consistent framework and avoiding the "complexity trap", which is essential for a better understanding of vegetation dynamics under climate change.

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Competing Interests

The authors declare that they have no competing financial interests.

Authors' Contributions

OF, SPH, ÅB, UD, SPH, HW, WC, ER, and ICP contributed to the outline of the paper, OF led the writing process, RD, CEF, DF, ML, HW, ICP, KTR, ÅB and OF contributed display items or specific sections, and all authors contributed to the final version of the paper.

References

Achat, D. L., L. Augusto, A. Gallet-Budynek, and D. Loustau. 2016. Future challenges in coupled C–N–P cycle models for terrestrial ecosystems under global change: a review. Biogeochemistry **131**:173-202.

Adler, P. B., A. Fajardo, A. R. Kleinhesselink, and N. J. B. Kraft. 2013. Trait-based tests of coexistence mechanisms. Ecology Letters **16**:1294-1306.

Bertram, J., and R. C. Dewar. 2013. Statistical patterns in tropical tree cover explained by the different water demand of individual trees and grasses. Ecology **94**:2138-2144.

Bloom, A. J. 1986. Plant economics. Trends in Ecology & Evolution **1**:98-100.

Bloomfield, K. J., I. C. Prentice, L. A. Cernusak, D. Eamus, B. E. Medlyn, R. Rumman, I. J. Wright, M. M. Boer, P. Cale, J. Cleverly, J. J. G. Egerton, D. S. Ellsworth, B. J. Evans, L. S. Hayes, M. F. Hutchinson, M. J. Liddell, C. Macfarlane, W. S. Meyer, H. F. Togashi, T. Wardlaw, L. Zhu, and O. K. Atkin. 2019. The validity of optimal leaf traits modelled on environmental conditions. New Phytologist **221**:1409-1423.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. MacE, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature **486**:59-67.

Chen, J. L., and J. F. Reynolds. 1997. A coordination model of whole-plant carbon allocation in relation to water stress. Annals of Botany **80**:45-55.

Chevin, L.-M., R. Lande, and G. M. Mace. 2010. Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLoS Biology **8**:e1000357.

Clark, J. S. 2016. Why species tell more about traits than traits about species: predictive analysis. Ecology **97**:1979-1993.

Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. Ecology Letters **10**:647-659.

Craven, D., N. Eisenhauer, W. D. Pearse, Y. Hautier, F. Isbell, C. Roscher, M. Bahn, C. Beierkuhnlein, G. Bönisch, N. Buchmann, C. Byun, J. A. Catford, B. E. L. Cerabolini, J. H. C. Cornelissen, J. M. Craine, E. De Luca, A. Ebeling, J. N. Griffin, A. Hector, J. Hines, A. Jentsch, J. Kattge, J. Kreyling, V. Lanta, N. Lemoine, S. T. Meyer, V. Minden, V. Onipchenko, H. W. Polley, P. B. Reich, J. van Ruijven, B. Schamp, M. D. Smith, N. A. Soudzilovskaia, D. Tilman, A. Weigelt, B. Wilsey, and P. Manning. 2018. Multiple facets of biodiversity drive the diversity–stability relationship. Nature Ecology & Evolution **2**:1579-1587.

de Almeida Castanho, A. D., D. Galbraith, K. Zhang, M. T. Coe, M. H. Costa, and P. Moorcroft. 2016. Changing Amazon biomass and the role of atmospheric CO_2 concentration, climate, and land use. Global Biogeochemical Cycles **30**:18-39.

De Kauwe, M. G., J. Kala, Y. S. Lin, A. J. Pitman, B. E. Medlyn, R. A. Duursma, G. Abramowitz, Y. P. Wang, and D. G. Miralles. 2015. A test of an optimal stomatal conductance scheme within the CABLE land surface model. Geosci. Model Dev. **8**:431-452.

Dewar, R., A. Mauranen, A. Mäkelä, T. Hölttä, B. Medlyn, and T. Vesala. 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.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet'ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce,

B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. Nature **529**:167-171.

Dong, N., I. Colin Prentice, B. Evans, S. Caddy-Retalic, A. Lowe, and I. Wright. 2017. Leaf nitrogen from first principles: field evidence for adaptive variation with climate. Biogeosciences **14**:481–495.

Dybzinski, R., C. Farrior, A. Wolf, P. B. Reich, and S. W. Pacala. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: An analytically tractable, individual-based model and quantitative comparisons to data. American Naturalist **177**:153-166.

Eller, C. B., L. Rowland, R. S. Oliveira, P. R. L. Bittencourt, F. V. Barros, A. C. L. da Costa, P. Meir, A. D. Friend, M. Mencuccini, S. Sitch, and P. Cox. 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: Biological Sciences **373**:20170315.

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

Farrior, C., S. Bohlman, S. Hubbell, and S. W. Pacala. 2016. Dominance of the suppressed: Power-law size structure in tropical forests. Science **351**:155-157.

Farrior, C. E. 2019. Theory predicts plants grow roots to compete with only their closest neighbours. Proceedings of the Royal Society B: Biological Sciences **286**:20191129.

Farrior, C. E., I. Rodriguez-Iturbe, R. Dybzinski, S. A. Levin, and S. W. Pacala. 2015. Decreased water limitation under elevated CO2 amplifies potential for forest carbon sinks. Proceedings of the National Academy of Sciences, USA **112**:7213-7218.

Farrior, C. E., D. Tilman, R. Dybzinski, P. B. Reich, S. A. Levin, and S. W. Pacala. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. Ecology **94**:2505-2517.

Favier, C., J. Chave, A. Fabing, D. Schwartz, and M. A. Dubois. 2004. Modelling forest–savanna mosaic dynamics in man-influenced environments: effects of fire, climate and soil heterogeneity. Ecological Modelling **171**:85-102.

Fisher, J. B., D. N. Huntzinger, C. R. Schwalm, and S. Sitch. 2014. Modeling the Terrestrial Biosphere. Annual Review of Environment and Resources **39**:91-123.

Fisher, R. A., C. D. Koven, W. R. L. Anderegg, B. O. Christoffersen, M. C. Dietze, C. E. Farrior, J. A. Holm, G. C. Hurtt, R. G. Knox, P. J. Lawrence, J. W. Lichstein, M. Longo, A. M. Matheny, D. Medvigy, H. C. Muller-Landau, T. L. Powell, S. P. Serbin, H. Sato, J. K. Shuman, B. Smith, A. T. Trugman, T. Viskari, H. Verbeeck, E. Weng, C. Xu, X. Xu, T. Zhang, and P. R. Moorcroft. 2018. Vegetation demographics in Earth System Models: A review of progress and priorities. Global Change Biology **24**:35– 54.

Fisher, R. A., S. Muszala, M. Verteinstein, P. Lawrence, C. Xu, N. G. McDowell, R. G. Knox, C. Koven, J. Holm, B. M. Rogers, A. Spessa, D. Lawrence, and G. Bonan. 2015. Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). Geoscientific Model Development **8**:3593-3619.

Follows, M. J., S. Dutkiewicz, S. Grant, and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. Science **315**:1843-1846.

Franklin, O. 2007. Optimal nitrogen allocation controls tree responses to elevated CO 2. New Phytologist **174**:811-822.

Franklin, O., J. Johansson, R. C. Dewar, U. Dieckmann, R. E. McMurtrie, Å. Brännström, and R. Dybzinski. 2012. Modeling carbon allocation in trees: a search for principles. Tree Physiology **32**:648-666.

Franklin, O., R. E. McMurtrie, C. M. Iversen, K. Y. Crous, A. C. Finzi, D. T. Tissue, D. S. Ellsworth, R. Oren, and R. J. Norby. 2009. Forest fine-root production and nitrogen use under elevated CO2: Contrasting

responses in evergreen and deciduous trees explained by a common principle. Global Change Biology **15**:132–144.

Franklin, O., T. Näsholm, P. Högberg, and M. N. Högberg. 2014a. Forests trapped in nitrogen limitation – an ecological market perspective on ectomycorrhizal symbiosis. New Phytologist **203**:657-666.

Franklin, O., S. Palmroth, and T. Näsholm. 2014b. How eco-evolutionary principles can guide tree breeding and tree biotechnology for enhanced productivity. Tree Physiology **34**:1149-1166.

Franks, S. J., S. Sim, and A. E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proceedings of the National Academy of Sciences, USA **104**:1278-1282.

Fyllas, N., E. Gloor, L. Mercado, S. Sitch, C. Quesada, T. Domingues, D. Galbraith, A. Torre-Lezama, E. Vilanova, and H. Ramírez-Angulo. 2014. Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v. 1). Geoscientific Model Development **7**:1251-1269.

Gaillard, C., L. Langan, M. Pfeiffer, D. Kumar, C. Martens, S. I. Higgins, and S. Scheiter. 2018. African shrub distribution emerges via a trade-off between height and sapwood conductivity. Journal of Biogeography **45**:2815-2826.

García-Palacios, P., N. Gross, J. Gaitán, and F. T. Maestre. 2018. Climate mediates the biodiversity–ecosystem stability relationship globally. Proceedings of the National Academy of Sciences.

Getzin, S., K. Wiegand, and I. Schöning. 2012. Assessing biodiversity in forests using very high-resolution images and unmanned aerial vehicles. Methods in Ecology and Evolution **3**:397-404.

Gilad, E., J. von Hardenberg, A. Provenzale, M. Shachak, and E. Meron. 2007. A mathematical model of plants as ecosystem engineers. Journal of Theoretical Biology **244**:680-691.

Glenn, E., A. Huete, P. Nagler, and S. G. Nelson. 2008. Relationship Between Remotely-sensed Vegetation Indices, Canopy Attributes and Plant Physiological Processes: What Vegetation Indices Can and Cannot Tell Us About the Landscape. Sensors **8**:2136-2160.

Guswa, A. J. 2010. Effect of plant uptake strategy on the water− optimal root depth. Water Resources Research **46**.

Hikosaka, K., and N. P. R. Anten. 2012. An evolutionary game of leaf dynamics and its consequences for canopy structure. Functional Ecology **26**:1024-1032.

Hofbauer, J., and K. Sigmund. 1988. The theory of evolution and dynamical systems. Mathematical aspects of selection. Cambridge University Press, London/New York.

Huang, Y., S. Gerber, T. Huang, and J. W. Lichstein. 2016. Evaluating the drought response of CMIP5 models using global gross primary productivity, leaf area, precipitation, and soil moisture data. Global Biogeochemical Cycles **30**:1827-1846.

Isbell, F., J. Cowles, L. E. Dee, M. Loreau, P. B. Reich, A. Gonzalez, A. Hector, and B. Schmid. 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecology Letters.

Jaynes, E. T. 2003. Probability theory: the logic of science. Cambridge university press.

Jump, A. S., and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters **8**:1010-1020.

Kennedy, D., S. Swenson, K. W. Oleson, D. M. Lawrence, R. Fisher, A. C. Lola da Costa, and P. Gentine. 2019. Implementing Plant Hydraulics in the Community Land Model, Version 5. Journal of Advances in Modeling Earth Systems **11**:485-513.

Kichenin, E., D. A. Wardle, D. A. Peltzer, C. W. Morse, and G. T. Freschet. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Functional Ecology **27**:1254-1261.

King, D. A. 1990. The adaptive significance of tree height. American Naturalist **135**:809-828.

Kleidon, A., K. Fraedrich, and C. Low. 2007. Multiple steady-states in the terrestrial atmosphere-biosphere system: a result of a discrete vegetation classification? Biogeosciences **4**:707-714.

Langan, L., S. I. Higgins, and S. Scheiter. 2017. Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest–savanna boundary in South America? Journal of Biogeography **44**:2319-2330.

Laughlin, D. C., and J. Messier. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology & Evolution **30**:487-496.

Lavorel, S., S. Díaz, J. H. C. Cornelissen, E. Garnier, S. P. Harrison, S. McIntyre, J. G. Pausas, N. Pérez-Harguindeguy, C. Roumet, and C. Urcelay. 2007. Plant functional types: are we getting any closer to the Holy Grail? Pages 149-164 *in* J. G. Canadell, D. E. Pataki, and L. F. Pitelka, editors. Terrestrial ecosystems in a changing world. Springer, Berlin.

Loreau, M. 2010. From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46). Princeton University Press.

Maire, V., N. Gross, D. Hill, R. Martin, C. Wirth, I. J. Wright, and J. F. Soussana. 2013. Disentangling Coordination among Functional Traits Using an Individual-Centred Model: Impact on Plant Performance at Intra- and Inter-Specific Levels. PLoS ONE **8**.

Manzoni, S., G. Vico, S. Palmroth, A. Porporato, and G. Katul. 2013. Optimization of stomatal conductance for maximum carbon gain under dynamic soil moisture. Advances in Water Resources **62**:90-105.

Marks, C. O. 2007. THE CAUSES OF VARIATION IN TREE SEEDLING TRAITS: THE ROLES OF ENVIRONMENTAL SELECTION VERSUS CHANCE. Evolution **61**:455-469.

McConnaughay, K., and J. Coleman. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology **80**:2581-2593.

McMurtrie, R. E., and R. C. Dewar. 2011. Leaf-trait variation explained by the hypothesis that plants maximize their canopy carbon export over the lifespan of leaves. Tree Physiology **31**:1007-1023.

McNickle, G. G., M. A. Gonzalez-Meler, D. J. Lynch, J. L. Baltzer, and J. S. Brown. 2016. The world's biomes and primary production as a triple tragedy of the commons foraging game played among plants. Proceedings of the Royal Society of London, Series B: Biological Sciences **283**.

Medlyn, B. E., R. A. Duursma, D. Eamus, D. S. Ellsworth, I. C. Prentice, C. V. Barton, K. Y. Crous, P. De Angelis, M. Freeman, and L. Wingate. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. Global Change Biology **17**:2134-2144.

Medlyn, B. E., S. Zaehle, M. G. De Kauwe, A. P. Walker, M. C. Dietze, P. J. Hanson, T. Hickler, A. K. Jain, Y. Luo, W. Parton, I. C. Prentice, P. E. Thornton, S. Wang, Y. P. Wang, E. Weng, C. M. Iversen, H. R. McCarthy, J. M. Warren, R. Oren, and R. J. Norby. 2015. Using ecosystem experiments to improve vegetation models. Nature Climate Change **5**:528-534.

Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. Journal of Geophysical Research: Biogeosciences **114**.

Meng, T.-T., H. Wang, S. P. Harrison, I. Prentice, J. Ni, and G. Wang. 2015. Responses of leaf traits to climatic gradients: adaptive variation versus compositional shifts. Biogeosciences **12**:5339-5352.

Meron, E. 2012. Pattern-formation approach to modelling spatially extended ecosystems. Ecological Modelling **234**:70-82.

Meron, E. 2016. Pattern formation – A missing link in the study of ecosystem response to environmental changes. Mathematical Biosciences **271**:1-18.

Montané, F., A. M. Fox, A. F. Arellano, N. MacBean, M. R. Alexander, A. Dye, D. A. Bishop, V. Trouet, F. Babst, A. E. Hessl, N. Pederson, P. D. Blanken, G. Bohrer, C. M. Gough, M. E. Litvak, K. A. Novick, R. P. Phillips, J. D. Wood, and D. J. P. Moore. 2017. Evaluating the effect of alternative carbon allocation schemes in

731 a land surface model (CLM4.5) on carbon fluxes, pools, and turnover in temperate forests. Geosci.
732 Model Dev. **10**:3499-3517.

733 Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala. 2001. A method for scaling vegetation dynamics: The ecosystem
734 demography model (ED). Ecological Monographs **71**:557-586.

735 Niinemets, U., T. F. Keenan, and L. Hallik. 2015. A worldwide analysis of within-canopy variations in leaf
736 structural, chemical and physiological traits across plant functional types. New Phytologist **205**:973-
737 993.

738 Pavlick, R., D. T. Drewry, K. Bohn, B. Reu, and A. Kleidon. 2013. The Jena Diversity-Dynamic Global Vegetation
739 Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and
740 biogeochemistry based on plant functional trade-offs. Biogeosciences **10**:4137-4177.

741 Prentice, I. C. 1998. Ecology and the earth system. Pages 219-240 *in* H. J. Schellnhuber and V. Wenzel, editors.
742 Earth System Analysis. Springer, Potsdam Institute for Climate Impact Research

743 Prentice, I. C., and S. A. Cowling. 2013. Dynamic Global Vegetation Models. Pages 670-689 *in* S. A. Levin, editor.
744 Encyclopedia of Biodiversity (Second Edition). Academic Press, Waltham.

745 Prentice, I. C., X. Liang, B. E. Medlyn, and Y. P. Wang. 2015. Reliable, robust and realistic: the three R's of next-
746 generation land-surface modelling. Atmos. Chem. Phys. **15**:5987-6005.

747 Pugh, T. A. M., C. D. Jones, C. Huntingford, C. Burton, A. Arneth, V. Brovkin, P. Ciais, M. Lomas, E. Robertson,
748 S. L. Piao, and S. Sitch. 2018. A Large Committed Long-Term Sink of Carbon due to Vegetation
749 Dynamics. Earth's Future **6**:1413-1432.

750 Purves, D. W., J. W. Lichstein, N. Strigul, and S. W. Pacala. 2008. Predicting and understanding forest dynamics
751 using a simple tractable model. Proceedings of the National Academy of Sciences of the United States
752 of America **105**:17018-17022.

753 Reich, P. B. 2014. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. Journal of Ecology
754 **102**:275-301.

755 Rietkerk, M., S. C. Dekker, P. C. De Ruiter, and J. Van De Koppel. 2004. Self-organized patchiness and
756 catastrophic shifts in ecosystems. Science **305**:1926-1929.

757 Sakschewski, B., W. von Bloh, A. Boit, L. Poorter, M. Peña-Claros, J. Heinke, J. Joshi, and K. Thonicke. 2016.
758 Resilience of Amazon forests emerges from plant trait diversity. Nature Climate Change **6**:1032.

759 Scheepens, J. F., E. S. Frei, and J. Stöcklin. 2010. Genotypic and environmental variation in specific leaf area in
760 a widespread Alpine plant after transplantation to different altitudes. Oecologia **164**:141-150.

761 Scheiter, S., L. Langan, and S. I. Higgins. 2013. Next-generation dynamic global vegetation models: Learning
762 from community ecology. New Phytologist **198**:957-969.

763 Schymanski, S. J., M. L. Roderick, and M. Sivapalan. 2015. Using an optimality model to understand medium
764 and long-term responses of vegetation water use to elevated atmospheric CO2 concentrations. AoB
765 PLANTS **7**:plv060-plv060.

766 Schymanski, S. J., M. Sivapalan, M. Roderick, L. B. Hutley, and J. Beringer. 2009. An optimality-based model of
767 the dynamic feedbacks between natural vegetation and the water balance. Water Resources Research
768 **45**.

769 Shipley, B., D. Vile, and É. Garnier. 2006. From Plant Traits to Plant Communities: A Statistical Mechanistic
770 Approach to Biodiversity. Science **314**:812-814.

771 Strigul, N., D. Pristinski, D. Purves, J. Dushoff, and S. Pacala. 2008. Scaling from trees to forests: Tractable
772 macroscopic equations for forest dynamics. Ecological Monographs **78**:523-545.

773 Sulman, B. N., E. Shevliakova, E. R. Brzostek, S. N. Kivlin, S. Malyshev, D. N. Menge, and X. Zhang. 2019. Diverse
774 mycorrhizal associations enhance terrestrial C storage in a global model. Global Biogeochemical
775 Cycles.

776 Thornley, J. H. M. 1998. Modelling Shoot:Root Relations: the Only Way Forward? Annals of Botany **81**:165-
777 171.

778 Thurner, M., C. Beer, P. Ciais, A. D. Friend, A. Ito, A. Kleidon, M. R. Lomas, S. Quegan, T. T. Rademacher, S.
779 Schaphoff, M. Tum, A. Wiltshire, and N. Carvalhais. 2017. Evaluation of climate-related carbon
780 turnover processes in global vegetation models for boreal and temperate forests. Global Change
781 Biology:n/a-n/a.

782 Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The Influence of Functional Diversity
783 and Composition on Ecosystem Processes. Science **277**:1300-1302.

784 Valentine, H. T., and A. Mäkelä. 2012. Modeling forest stand dynamics from optimal balances of carbon and
785 nitrogen. New Phytologist **194**:961-971.

786 van Bodegom, P. M., J. C. Douma, and L. M. Verheijen. 2014. A fully traits-based approach to modeling global
787 vegetation distribution. Proceedings of the National Academy of Sciences **111**:13733-13738.

788 Walker, A. P., S. Zaehle, B. E. Medlyn, M. G. De Kauwe, S. Asao, T. Hickler, W. Parton, D. M. Ricciuto, Y. P. Wang,
789 D. Wårlind, and R. J. Norby. 2015. Predicting long-term carbon sequestration in response to CO_2
790 enrichment: How and why do current ecosystem models differ? Global Biogeochemical Cycles **29**:476–
791 495.

792 Wang, H., I. C. Prentice, T. F. Keenan, T. W. Davis, I. J. Wright, W. K. Cornwell, B. J. Evans, and C. Peng. 2017.
793 Towards a universal model for carbon dioxide uptake by plants. Nature Plants **3**:734-741.

794 Weiner, J., P. Stoll, H. Muller-Landau, and A. Jasentuliyana. 2001. The effects of density, spatial pattern, and
795 competitive symmetry on size variation in simulated plant populations. American Naturalist **158**:438-
796 450.

797 Weng, E., S. Malyshev, J. Lichstein, C. Farrior, R. Dybzinski, T. Zhang, E. Shevliakova, and S. Pacala. 2015. Scaling
798 from individual trees to forests in an Earth system modeling framework using a mathematically
799 tractable model of height-structured competition. Biogeosciences **12**:2655-2694.

800 Whitley, R., J. Beringer, L. B. Hutley, G. Abramowitz, M. G. De Kauwe, B. Evans, V. Haverd, L. Li, C. Moore, and
801 Y. Ryu. 2017. Challenges and opportunities in land surface modelling of savanna ecosystems.
802 Biogeosciences.

803 Wolf, A., W. R. L. Anderegg, and S. W. Pacala. 2016. Optimal stomatal behavior with competition for water and
804 risk of hydraulic impairment. Proceedings of the National Academy of Sciences **113**:E7222-E7230.

805 Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C.
806 Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee,
807 W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L.
808 Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The
809 worldwide leaf economics spectrum. Nature **428**:821-827.

810 Xia, J., W. Yuan, Y.-P. Wang, and Q. Zhang. 2017. Adaptive Carbon Allocation by Plants Enhances the Terrestrial
811 Carbon Sink. Scientific Reports **7**:3341.

812 Xu, C., R. Fisher, S. D. Wullschleger, C. J. Wilson, M. Cai, and N. G. McDowell. 2012. Toward a Mechanistic
813 Modeling of Nitrogen Limitation on Vegetation Dynamics. PLoS ONE **7**:e37914.

814 Xu, X., D. Medvigy, J. S. Powers, J. M. Becknell, and K. Guan. 2016. Diversity in plant hydraulic traits explains
815 seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. New
816 Phytologist **212**:80-95.

817 Yang, J., M. Cao, and N. G. Swenson. 2018. Why Functional Traits Do Not Predict Tree Demographic Rates.
818 Trends in Ecology & Evolution **33**:326-336.

819 Yang, Y., R. J. Donohue, and T. R. McVicar. 2016. Global estimation of effective plant rooting depth:
820 Implications for hydrological modeling. Water Resources Research **52**:8260-8276.

821

822