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Modelling water fluxes in plants: from tissues to biosphere

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Summary

Models of plant water fluxes have evolved from studies focussed on understanding the detailed structure and functioning of specific components of the soil–plant–atmosphere (SPA) continuum to architectures often incorporated inside eco-hydrological and terrestrial biosphere (TB) model schemes. We review here the historical evolution of this field, examine the basic structure of a simplified individual-based model of plant water transport, highlight selected applications for specific ecological problems and conclude by examining outstanding issues requiring further improvements in modelling vegetation water fluxes. We particularly emphasise issues related to the scaling from tissue-level traits to individual-based predictions of water transport, the representation of nonlinear and hysteretic behaviour in soil–xylem hydraulics and the need to incorporate knowledge of hydraulics

within broader frameworks of plant ecological strategies and their consequences for predicting community demography and dynamics.

Key words: Hydraulics, water relations, water transport, modelling, mechanistic models, prediction, xylem, scaling.

I. Introduction

A Tansley review published in New Phytologist more than 25 years ago (Tyree & Ewers, 1991) set out the fundamental concepts of plant hydraulic architecture of trees and other woody plants (Zimmermann, 1983) and implemented them in a discretized, variable resistance-capacitance model to interpret daily patterns of plant water status. Since then, the quantitative description of water flows in plants has become instrumental in developing eco-hydrological (e.g., Williams *et al.*, 1996; Manzoni *et al.*, 2014), dynamic vegetation and terrestrial biosphere (TB) models (Hickler *et al.*, 2006; Bonan *et al.*, 2014; Naudts *et al.*, 2015). Plant hydraulics is contributing directly to the analysis of the effects of global change on plants (e.g., Anderegg *et al.*, 2015, Liu *et al.*, 2017) and to studies of the terrestrial water cycle (Pappas *et al.*, 2014; Fatichi *et al.*, 2016; Xu *et al.*, 2016; Anderegg *et al.*, 2018a).

The general objective of this review is to provide an overview of how processes governing water fluxes in plants have been represented in mathematical models of soil-plant-atmosphere (SPA) water transport, with a particular focus on the plant component. Since the review by Tyree & Ewers (1991), theories and concepts relevant for the understanding of water flow in plants have considerably advanced and this progress has shaped how models of plant water flow represent these processes.

The literature on modelling water transport through plants has exploded in the last two decades and a complete review of this field is unnecessary (Fatichi *et al.*, 2016; Matheny *et al.*, 2017b). We elected instead to emphasise the existing diversity of approaches at a range of scales to allow a critical comparison of how plant water transport can be modelled and to identify research lines that should be explored in the future to improve modelling of water transport through plants.

We structured the review in a hierarchical fashion to account for the different spatial and temporal scales represented in models (Figure 1), from those that are primarily focussed on a detailed description of compartments and flows within individual plants (tissue- and plants-centred models), to those representing water flows with a focus on the interactions between rainfall, soil hydrology and climate (synthetically, referred to as eco-hydrological models, either deterministic or using a stochastic approach), to models intended to represent water transport and water status in plants at the community and up to global scales. In many recent TB models, population dynamics modules have been incorporated that depend on 'functional' traits, including hydraulic ones (e.g., Fisher *et al.*, 2015; Xu *et al.*, 2016). TB models therefore provide opportunities to analyse feedbacks between plant hydraulics, community-level distributions of plant traits, vegetation dynamics and ecosystem and biosphere processes at broad spatial and temporal scales. Explicit representation of water flow inside plants is required to upscale the effects of water availability on individual-level recruitment, growth and mortality mechanistically (Fisher *et al.*, 2018; Xu *et al.*, 2016).

II. A brief history of modelling plant water fluxes

Modern quantitative theories of water transport in plants can be traced back to the early 20th century (Gradmann, 1928, and later van den Honert, 1948), when the concept of soil-plant-atmosphere (SPA) continuum was developed (Cowan, 1965, Philip, 1966, Molz, 1981). One of the first mathematical models describing water flows from the soil to a plant root in unsaturated soil was by Gardner (1960), who built on earlier work (Philip, 1955). The root was modelled as an infinitely long cylinder with constant radius and hydraulic properties. The first soil-plant hydraulic model based on resistance analogues run on a digital computer is possibly the one reported in Cowan (1965). It represented water transport as a network of resistances (impedances) from the soil to the atmosphere and simulated transport during the course of a day and during drying cycles as a function of rooting depth and density. The concepts of water 'supply function' and 'demand function' were presented, whereby supply limitations were largely determined by soil properties. Water transport through soils was known to show hysteretic behaviour, as the relationship between pressure head and water content was dependent on the history of drying-wetting events, a behaviour thought to be limited to the soil. In addition, the lack of empirical information on actual values of plant hydraulic resistances slowed down progress for many years. During the 1970s and 1980s, improvements were made in representing variable apparent root membrane permeability as a result of transpiration-driven solute drag (Fiscus, 1975), root shrinkage during drought reducing contact with soil (Herkelrath *et al.*, 1977) and a water front moving downward through the soil (Gardner, 1991). Parallel symplasmic and apoplastic pathways were also introduced (Molz, 1976) and later shown to lead to variable root hydraulic conductivity (Steudle, 2000). Hydraulic redistribution among soil layers and nonlinearities in plant axial conductance were not accounted for.

Advances in measuring sap flow, xylem hydraulic conductivity, water storage and stomatal conductance (e.g., Jarvis, 1976) led to models representing the links among these variables (Running *et al.*, 1975; Edwards *et al.*, 1986). Discovery of cavitation in xylem conduits (Milburn, 1966) and methods to quantify its effects (Edwards & Jarvis, 1982; Sperry *et al.*, 1988) led to the first models incorporating hydraulic architecture (Tyree, 1988) and later xylem embolism, and therefore nonlinearities in xylem hydraulics (Tyree & Sperry, 1988). Discussions of likelihood of refilling (Canny, 1997) pointed to the fact that significant hysteresis can occur in the relationships between xylem water potential and conductivity if refilling does not, or is slow to occur (Sperry *et al.*, 2003). Further important steps were made applying these concepts to make predictions of water and carbon fluxes at the ecosystem scale (Friend, 1995; Williams *et al.*, 1996). Important advances have taken place in a) constraining biomass allocation and net primary productivity using hydraulic properties and functional balance (Magnani *et al.*, 2000); b) employing within-day and seasonal variations in water storage and capacitance to predict effects on water fluxes (Loustau *et al.*, 1998) and on growth via measurements of tissue shrinkage and swelling (Steppe *et al.*, 2006); c) predicting likelihood of drought-induced mortality based on xylem vulnerability to embolism (Martínez-Vilalta *et al.*, 2002); d) predicting effects of belowground hydraulic redistribution via roots (Lee *et al.*, 2005; Quijano *et al.*, 2012); e) anticipating vertical root distribution as a function of water table depth, capillary rise and topography (Fan *et al.*, 2017) and water fluxes as a function of rooting depth (Matheny *et al.*, 2017a) and f) advancing understanding of stomatal behaviour via modelling of water and vapour fluxes in leaves (Peak & Mott, 2011; Rockwell *et al.*, 2014; Buckley, 2015). Moreover, xylem hydraulic properties and their variation with branch order constrain metabolic scaling laws emerging from fractal tree models (West *et al.*, 1999; Savage *et al.*, 2010). As process understanding improved, mathematical approaches to solve the water transport problem also developed, from the first models based on series of point conductances (electrical analogy) (van den Honert, 1948), to those employing the matrix flux potential approach (Kirchhoff transform) to account for continuous variations in water potential along homogenous stem segments (Sperry *et al.*, 1998; Sperry & Love, 2015), to more sophisticated numerical (e.g., Bohrer *et al.*, 2005; Janott *et al.*, 2011) and analytical (Couvreur *et al.*, 2018) solutions.

III. Main components of plant water transport models

Ecosystem and TB models have tended in the past to lump plant vascular transport into a single hydraulic resistance term, or ignore plant hydraulics altogether (see reviews by Anderson *et al.*, 2003; Fatichi *et al.*, 2016, for further details). In contrast, water transport and hydraulic architecture were developed in much detail in several tissue-scale (Arbogast *et al.*, 1993; Schulte & Costa, 1996; Aumann & Ford, 2002; Loepfe *et al.*, 2007) and individual-scale (Cowan, 1965; Sperry *et al.*, 1998; Fruh & Kurth, 1999; Chuang *et al.*, 2006; Hölttä *et al.*, 2009; De Schepper & Steppe, 2010) models of plant vascular transport and water fluxes, some of which are capable of resolving fractal-like hydraulic architecture inside plants (e.g., Bohrer *et al.*, 2005) or take advantage of detailed plant architectural measurements (Janott *et al.*, 2011). More recently, hydraulic modules have been included also in models operating at larger spatial and temporal scales. Some models operate at these scales by explicitly representing the many constituent individuals (individual-based), while others use a single, representative average individual (i.e., the ‘big-leaf’ approach) or a ‘cohort-based’ representation. Such hydraulic modules generally need three components: a) a description of hydraulic traits at the tissue scale (roots, stems, leaves); b) procedures and associated allometric parameters to scale up tissue-level properties to the whole plant and c) procedures linking the scaled-up hydraulic architecture to whole-plant water fluxes. Examples include plant-centred models (Sterck *et al.*, 2011), individual-based eco-hydrological models (e.g., TREES and TFS-Hydro, Mackay *et al.*, 2015; Christoffersen *et al.*, 2016), ‘big-leaf’ ecosystem models (e.g., SPA, Williams *et al.*, 1996) and TB models (Hickler *et al.*, 2006). For models operating at scales larger than the individual plant, there can also be procedures scaling the behaviour of the average individual or the distribution of individuals to the emerging cohort or stand (e.g., Christoffersen *et al.*, 2016; Xu *et al.*, 2016; Manoli *et al.*, 2017).

Tissue-level hydraulic traits

Extensive lists of plant water relations and hydraulics traits and a discussion of their relevance for modelling of plant water fluxes are given elsewhere (Matheny *et al.*, 2017b; Choat *et al.*, 2018). Tissue-level traits are commonly employed to obtain individual-level hydraulic properties because of the existence of databases containing large collections of empirical information on terminal units of plants, most often from hydraulic studies of detached xylem segments cut from young branches (Choat *et al.*, 2012) and increasingly leaves (Sack & Holbrook, 2006; Bartlett *et al.*, 2012) and roots (Choat *et al.*, 2012). This allows a representation of a number of plant processes that would otherwise be lumped into single parameters of unknown behaviour. Adopting a xylem-centric perspective (justified by current data availability), the 'minimum' set of hydraulic traits includes the specific conductivity of the xylem $k_{X,max}$ (at least at one position in the continuum, at some reference state under well-water conditions), the vulnerability to embolism of these tissue-level segments (e.g., water potential at 50%, $\psi_{X,50}$; at 12 and 88% loss of hydraulic conductivity $\psi_{X,12}$ and $\psi_{X,88}$; slope of vulnerability curves) and, at least, the maximum stomatal conductance of leaves $g_{S,max}$. Defining this minimum set is an active area of research, as it implies a hypothesis over the dominant axes of variation of hydraulic behaviour in plants, over which there is little consensus. Other traits can be introduced to increase model realism and generality at the expense of complexity, i.e., the hydraulic vulnerability, capacitance and/or water storage of leaves (Martin-StPaul *et al.*, 2017); the ratio between root area and leaf area (Sperry *et al.*, 1998); phloem capacitance (Zweifel *et al.*, 2005; De Schepper & Steppe, 2011; Pfautsch *et al.*, 2015) or xylem capacitance (e.g., Hölttä *et al.*, 2009); the minimum leaf cuticular conductance (Martin-StPaul *et al.*, 2017); the relationships between stomatal conductance, whole-leaf conductance and canopy conductance (e.g., Mallick *et al.*, 2016); the vulnerability to cavitation in separate organs (roots, stems, leaves) (e.g., Sperry & Love, 2015).

Leaving aside issues related to environmental heterogeneity in a canopy, scaling these traits to individual plants requires also a statement of how properties measured in terminal units relate to the same properties measured elsewhere in the plant.

Scaling-up procedures from tissues to whole plants

Water fluxes and stomatal conductance are whole-plant variables controlled by whole-plant architecture and physiology, hence tissue-level traits need to be scaled to individual level. Scaling-up from tissue to plant requires robust procedures to work out whole-plant conductance and whole-plant vulnerability curves (Sperry & Love, 2015; Couvreur *et al.*, 2018), such that variability in traits across plant organs are accounted for. Mathematically, the problem can be addressed (Savage *et al.*, 2010; Sperry & Love, 2015; Sperry *et al.*, 2017; Couvreur *et al.*, 2018), but the limited amount of information on vertical variation in hydraulic traits, whole-plant architecture and allometry (with a few exceptions) currently limits advances in this direction. By contrast, vertical variation in anatomical traits related to hydraulics has been studied (especially conduit diameter, e.g., Olson *et al.*, 2018), but comparative work linking these patterns to hydraulic performance is scant.

Scaling of tissue-level conductivity to whole-plant conductance can be done at a minimum using an Ohm's law analogy, i.e.: $g_{plant} = \frac{A_X\, k_X}{H}$, where g_{plant} and H are the hydraulic conductance of a plant from root surface to sites of evaporation and plant height (taken as surrogate of path length), respectively, while A_X and k_X refer to measurements of sapwood area and hydraulic conductivity per unit sapwood area at some reference location (e.g., Whitehead & Jarvis, 1981; Sterck *et al.*, 2011). More complex schemes may include corrections for conduit furcation and conduit tapering vertically within a plant to minimize the height effect inherent in the inverse relationship employed in the equation for g_{plant} (e.g., West *et al.*, 1999; Savage *et al.*, 2010; Christoffersen *et al.*, 2016).

Extra-xylary conductances are generally not incorporated in measures of whole-plant conductance, even though extra-xylary resistances in roots and leaves account for a very large, sometimes dominant fraction of whole-plant hydraulic resistance (Fiscus, 1975; Sack & Holbrook, 2006; Sack & Scoffoni, 2013). Additionally, the behaviour of leaf and root hydraulics with respect to plant water potential can be highly non-linear and hysteretic.

Different assumptions have been proposed to scale up the ratios of sapwood area to leaf area (Huber values, HV) from single segments to plants, communities and grid cells. At the plant scale, the simplest assumption is that plants behave entirely as pipe models, i.e., that the HV of an apical segment is conserved as one moves downward along the plant branching architecture (Shinozaki *et al.*, 1964; Savage *et al.*, 2010). As an alternative, Murray's hypothesis of energy consumption minimization can be adopted (e.g., McCulloh *et al.*, 2003). Few data are available to test these hypotheses cross-species. A reasonable assumption (supported by the findings given in Supplementary Data, Notes S1, Fig. S1) is that Huber values can vary across species but are conserved along the heights of a tree. This conclusion is consistent with the finding that, within individuals, the sums of stem cross-sectional areas are also broadly conserved across branching levels (e.g., Nikinmaa, 1992; van der Sande *et al.*, 2015). Developing larger datasets of the variability of HV and stem cross-sectional areas within trees is a priority to allow scaling HV from branches to trees.

Procedures to scale up curves of vulnerability to embolism within plants are not well established. Modelling (Hölttä *et al.*, 2011) analyses suggest that a vertically varying profile of $\psi_{X,50}$ (more negative $\psi_{X,50}$ values attained towards the top of the tree) may be realistic, consistent with the hypothesis of hydraulic vulnerability segmentation (see review of available data and theory in Couvreur *et al.*, 2018). However, some empirical reports contradict this hypothesis (e.g., Wason *et al.*, 2018), despite general trends for narrower conduits in leaves vs stems/roots. When data are available separately for roots, stems and leaves of a species, a segmented profile can be employed, with homogeneous parameterization along the lengths of these organs (e.g., Sperry & Love, 2015).

Finally, plant water potentials also vary systematically from roots to leaves. Discretized modelling of axial resistances (e.g., Hölttä *et al.*, 2006) can approximate these vertical profiles, but these schemes may be computationally expensive for large models. Alternatively, the Kirchhoff integral transform can be used. The Kirchhoff transform accounts for variable conductivity, resulting from fluxes associated with internal water potential gradients in a medium with homogenous properties. Cowan (1965) is credited as the first to employ the Kirchhoff transform in a model of water flow in soils towards the root (Van Lier *et al.*, 2009). The 'water supply' curve described above (Sperry *et al.*, 1998; Sperry & Love, 2015) assumes that there are enough conduits and pores between conduits to approximate the xylem medium as continuous – this amounts to assuming short conduits in a long stem, or highly discretized segments. Depending on its configuration, the Kirchhoff transform can also be computationally expensive.

Whatever approaches are chosen to estimate individual-level properties, scaling these traits to all plants in a community or a grid cell requires knowledge of the probability density functions (PDF) of additional variables, such as the stand-level, PFT (plant functional type) or pixel-level Huber values (ratio of conducting sapwood to subtended leaf area), tree heights, plant sapwood volumes (for traits related to capacitance), leaf areas (to upscale leaf traits) and root abundance and distribution with depth (cf., Sections **IV** and **V**).

Links between hydraulics, stomatal conductance and photosynthesis

With regard to the links between scaled-up traits and stomatal behaviour, plant and eco-hydrological models have often represented stomatal conductance without any direct feedback from the hydraulic system, even when components of plant hydraulics were included. As a partial exception, the model SPA (Williams *et al.*, 1996; Fisher *et al.*, 2006; Bonan *et al.*, 2014) built upon earlier work (Jones & Sutherland, 1991; Tardieu & Davies, 1993) and coupled the maximization of carbon gains as a function of stomatal opening with the use of a threshold for stomatal closure at a critical water potential. Other models derive instead stomatal conductance from some modification of the Cowan & Farquhar (1977) marginal water use model (e.g., for two TB models, Kala *et al.*, 2015, Knauer *et al.*, 2015). Effects of soil drought on stomatal conductance are approximated using a sigmoid function of soil (reviewed in Smith *et al.*, 2014, Rogers *et al.*, 2017) or plant water availability (e.g., leaf water potential, Tuzet *et al.*, 2003). Finally, attempts have been made to combine demand limitations from the marginal water use model with the supply ('hydraulic') and other non-stomatal limitations (Manzoni *et al.*, 2013; Novick *et al.*, 2016; Dewar *et al.*, 2018), using optimization principles to incorporate feedbacks between hydraulic and photosynthetic traits (Table 1).

The Prentice *et al.* (2014) model follows the micro-economic principle that plants minimize a summed cost function of substitutable resources (here, water and nutrients) to obtain a unit product. The cost function is the minimum of the summed unit maintenance costs for carboxylation capacity and the transpiration pathway over some finite time interval (months to years) per unit of photosynthates. Substitution between long-term investments in photosynthesis versus hydraulics may thus be cost-neutral. In the Sperry *et al.* (2017) model, plants maximise the difference between relative photosynthetic gains and relative hydraulic risk (both on a 0-1 scale). These values are normalised relative to the maximum achievable photosynthetic rates (not capacity) and the hydraulic potential at the downstream end of the flow pathway (in principle, the leaf). The solution to this maximization problem is that the marginal (i.e., per unit of canopy pressure change) normalised carbon gain equals the marginal normalised hydraulic risk of losing conductance by embolisation, i.e., an instantaneous optimisation criterion, instead of a time-integrated one. Here, the maximum achievable photosynthetic rate is calculated at the critical maximum canopy pressure (most negative water potential) where canopy desiccation occurs, which implies that the maximum achievable photosynthetic rate will itself decline during drought. The model by Wolf *et al.* (2016) is similar to the one by Sperry *et al.* (2017) in the use of an instantaneous time scale and a maximization criterion based on the difference between gains and costs (risks). The main difference is that in this approach (cf., Anderegg *et al.*, 2018b), costs and gains are not normalised and the 'shadow' cost only depends upon leaf water potential (parabolic with a minimum at leaf water potential $\psi_L \rightarrow 0$), leaving unspecified whether it is determined by the instantaneous risk of conductance losses, osmotic adjustment, foregone photosynthetic production or phloem transport costs. Other costs (e.g., non-stomatal limitations, xylem conduit rebuilding, photosynthetic and/or hydraulic acclimation) are only indirectly accounted for in these approaches, by the fit to the observed water potential regulation of stomatal conductance during drought. Finally, Huang *et al.* (2018) developed ideas by Hölttä *et al.* (2017) to incorporate a stomatal optimization scheme accounting for both xylem and phloem transport limitations. In this approach, low water potentials limit stomatal aperture twice, i.e., via losses of xylem hydraulic conductance and via reduced phloem competition for xylem water, reducing sucrose transport out of the leaves during droughts (via reduced phloem turgor). The main advantage of optimality approaches is that many fitted parameters are substituted by (in principle) measurable hydraulic (xylem and phloem) and photosynthetic traits, although some calibration is often still required (cf., Table 1). Incorporating belowground hydraulics currently requires either empirical calibration or the setting of empirical coefficients.

Summary

Overall, understanding of the main biological scaling patterns related to the biophysics of water transport is still incomplete. However, mechanistic modelling of plant hydraulics over time-scales much longer than a few hours and spatial scales larger than a single plant is now possible. Major progress has been made in modelling lags in water transport processes (i.e., between soil and xylem, between xylem and leaves, in stomatal aperture), e.g., by using porous media models to represent water fluxes, while conserving mass (e.g., Bohrer *et al.*, 2005; Christoffersen *et al.*, 2016; Mirfenderesgi *et al.*, 2016), as opposed to classic resistance/capacitor models (cf., discussion in Chuang *et al.*, 2006). These temporal lags in plant fluxes and water status caused by storage can also lead to hysteretic behaviour, but this is qualitatively different from the processes mentioned before, which are caused instead by changes in soil properties (water content/conductivity relationship) or plant traits (hydraulic conductivity/xylem water potential relationship) in response to the environment.

IV. Stand-scale water fluxes and coupling to climate and soil

Water and carbon fluxes

We discuss here one approach to describe long-term mean plant water fluxes at the stand-scale by means of a stochastic model. This approach builds on the tissue- and plant-scale models described in the previous sections, and extends the predictions of water fluxes to account for variable environmental conditions at the stand-scale. The main motivation is to assess the statistical properties of water fluxes rather than simulating the outcome of a specific time series of environmental conditions. Also, by explicitly linking a minimal description of plant hydraulic properties to dynamic changes in soil moisture, this modelling approach bridges the gap between plant physiological and hydrologic models. Other models provide a more realistic description of soil-plant-atmosphere couplings (Tardieu & Davies, 1993; Launiainen *et al.*, 2011; Schymanski *et al.*, 2013; Fatichi *et al.*, 2016; Huang *et al.*, 2017; Feng *et al.*, 2018), but require extensive numerical experiments. The minimal approach presented here is based on a simple SPA continuum model that couples daily water fluxes to variable soil water availability and atmospheric conditions (Figure 2a-b). Daily values are then scaled-up in time by accounting for randomness in rainfall occurrences (Figure 2c-d). While details are reported elsewhere (Rodriguez-Iturbe & Porporato, 2005; Manzoni *et al.*, 2014; Vico *et al.*, 2017), a short description is provided here (cf., Supplementary Data, Notes S2).

Water transport from the soil to the leaves is driven by water potential differences through a series of conductances (soil-root and root-leaf), as described in previous sections. Each conductance is characterized by tissue-level properties that are scaled up to the stand-scale multiplying them by the corresponding tissue area per unit ground area – e.g., sapwood and leaf area indices. The root-leaf conductance can be expressed as in Section *Scaling-up procedures from tissues to whole plants*, where the sapwood area-specific conductivity may be reduced by cavitation as the xylem water potential decreases. The xylem water potential is conservatively approximated by the leaf ψ_L, consistent with using cavitation curves typically measured in terminal twigs, so that xylem vulnerability curves are denoted by $k_X(\psi_L)$ (Figure 2a). Evaporation from the stomatal cavity is driven by the vapour pressure deficit (VPD) around the leaf (assuming a well-coupled canopy and that air in the stomatal cavity is saturated), and mediated by stomatal conductance (Hari et al., 1986), which is in turn expressed as a function of leaf water potential (equal to leaf pressure when gravity is neglected), $g_S(\psi_L)$ (Figure 2a). Linking stomatal conductance to leaf water potential allows capturing stomatal closure due to increasing VPD, which causes higher transpiration rates and thus lowers ψ_L, or decreasing soil moisture, which also lowers ψ_L at a given transpiration rate. While the risk-gain stomatal optimization theory (Wolf *et al.*, 2016; Sperry *et al.*, 2017) could apply here (cf., Section *Links between hydraulics, stomatal conductance and photosynthesis*), and $k_X(\psi_L)$ and $g_S(\psi_L)$ relations are in general sigmoidal, a simple piecewise linear function $g_S(\psi_L)$ is adopted for analytical tractability (Manzoni *et al.*, 2014). The maximum xylem conductivity and maximum stomatal conductance are denoted by $k_{X,max}$ and $g_{S,max}$, whereas the water potential levels at 50% loss of xylem conductivity and at 50% stomatal closure are denoted as before by $\psi_{X,50}$ (equivalent to P50) and $\psi_{S,50}$ (Figure 2a).

Using the relations $k_X(\psi_L)$ and $g_S(\psi_L)$, it is possible to respectively calculate the water flow from the soil to the leaves ($\sim k_X(\psi_L) \times (\psi_S - \psi_L)$, representing the water supply) and the transpiration rate ($\sim g_S(\psi_L) \times \mathrm{VPD}$, representing the atmospheric water demand). Because the relations $k_X(\psi_L)$ and $g_S(\psi_L)$ are specified (Figure 2a), by equating water demand and supply, the leaf water potential (the only unknown) can be obtained. Finally, knowledge of ψ_L allows finding an explicit relation between transpiration rate and soil water potential (and thereby soil moisture), tissue-level hydraulic conductances, sapwood- and leaf-area indices, and soil properties (Figure 2a-b). While in this example only water fluxes are calculated, a stand-level carbon balance can be coupled to the water fluxes to calculate net primary productivity and assess trade-offs among water use strategies. This would require accounting for limiting factors such as CO_2, light, temperature, and nutrients, and for carbon allocation patterns.

This minimal representation of water transport in plants allows for full analytical tractability, but rests on the assumptions that plant water storage, the effect of gravity, and the temporal variability of environmental conditions other than rainfall and soil moisture can be neglected. The first assumption is reasonable especially at the daily time scale and under moist conditions, while the second one especially so for relatively short plants, but even in that case the progressive development of cavitation along the hydraulic pathway cannot be captured (Couvreur et al., 2018). Xylem vulnerability and stomatal closure curves are assumed static and piecewise linear functions of leaf water potential. This assumption implies that $\psi_{X,50}$, $\psi_{S,50}$, $k_{X,max}$ and $g_{S,max}$ are treated as invariant 'traits'. A more mechanistic approach would instead consider these curves as outcomes of the underlying dynamics of xylem cavitation and refilling, and compound stomatal responses to VPD and soil drying (e.g., Tardieu & Davies, 1993; Buckley *et al.*, 2003). When piecewise linear $k_X(\psi_L)$ and $g_S(\psi_L)$ are used, ψ_L is obtained analytically, otherwise a numerical scheme can be implemented, to avoid underestimating the sensitivity of xylem conductivity and stomatal conductance to changes in water potential. Finally, carry-over effects of cavitation events due to incomplete xylem refilling are not captured (e.g., Feng *et al.*, 2018).

Coupling to climatic conditions

Once whole-plant properties are predicted via a suitable scaling scheme from the tissue-level traits, they can be coupled to descriptors of site climatic conditions. Scaled-up hydraulic models describing leaf-to-canopy gas exchanges, plant growth, primary productivity, and crop yields are confronted with environmental variability occurring at virtually all temporal and spatial scales (Katul *et al.*, 2007). Numerical approaches employ observed time trajectories of all the relevant variables to drive process-based or empirical sub-models of plant exchanges and growth (e.g., Launiainen *et al.*, 2011; Schymanski *et al.*, 2013). While measured time series are realistic drivers of modelled plant processes, they are also limited to the duration of the measurement period, and therefore might not represent the full spectrum of possible variations – especially extreme but rare events. Treating environmental drivers as stochastic variables addresses this limitation by accounting in a more complete way for the intermittent and unpredictable nature of environmental variability (Cowan, 1986; Rodriguez-Iturbe & Porporato, 2005; Katul *et al.*, 2007). These approaches provide a representation of the mean and variability in plant processes that is particularly suitable to address the question – how does variability in environmental conditions (water availability in particular) translate into variability in plant and ecosystem processes?

Several coupled soil-plant stochastic models have been proposed to investigate the propagation of soil moisture fluctuations on long-term mean transpiration and plant water stress (Rodriguez-Iturbe & Porporato, 2005), optimality in the responses of stomatal conductance (Cowan, 1986; Mäkelä et al., 1996), leaf phenology (Vico et al., 2017) and rooting depth (Guswa, 2010), the emergence of functional trait coordination (Manzoni *et al.*, 2014), and competition dynamics (Farrior et al., 2015). All these models are based on comparable stochastic approaches once the relations between the fluxes (i.e., water) and the environmental conditions (soil moisture) of interest are obtained (Figure 2a, b, in our case as described in Section *Water and carbon fluxes*).

Daily gas exchange rates vary because of the random dynamics of soil moisture. Rainfall events replenish the soil moisture pool, but the timing and rain depths are random (Figure 2c). Therefore, to calculate the growing season transpiration and net primary productivity, such randomness needs to be accounted for using a stochastic soil moisture balance, yielding probability density functions of water and carbon fluxes. As a result, the mean growing season fluxes depend on the statistical properties of rainfall events.

Therefore, altering the statistical properties of rainfall allows exploring how mean and variability of transpiration rate and net primary productivity change along spatial transects (statistics change in space) and through time due to climatic shifts (statistics change in time, Figure 2d). With this approach, long-term shifts in the statistical properties of gas exchange rates are quantified via a set of closed-form equations for the water balance (in particular transpiration, E) and net primary productivity, parameterized based on the daily scale fluxes. In this way, the effects of plant traits on the long-term patterns of transpiration and productivity under different climatic regimes are assessed analytically (Figure 3).

The insight offered by this approach lies in exploring how plant traits and rainfall statistical properties not only co-determine the long-term mean transpiration rate <*E*>, but also how the sensitivity of each on <*E*> is modulated by the other. Figure 3 illustrates these points. The long-term mean transpiration rate $\langle E \rangle$ was calculated to illustrate how plant hydraulic traits and rainfall statistical properties affect this key component of the hydrologic cycle and proxy of several plant functions. The model was parameterized for a uniform tree stand (Table S1; Figure 3). The $\langle E \rangle$ is shown as a function of two parameter groups that represent the relative sensitivity and efficiency of water loss through the stomata relative to transport in the xylem: the ratio between water potential at 50% stomatal closure and at 50% loss of xylem conductivity ($\psi_{S,50}/\psi_{X,50}$, Figure 3a) and the ratio between maximum stomatal conductance and saturated sapwood hydraulic conductivity ($g_{S,max}/k_{X,max}$, Figure 3b), respectively.

Figure 3a shows that the $\langle E \rangle$ of a uniform stand increases as the two water potential levels at 50% loss of water transport capacity approach each other. This pattern is due to more effective use of water by plants that coordinate stomatal closure and loss of xylem conductivity (Manzoni *et al.*, 2014). As rainfall frequency is decreased (from solid to dotted curves), the $\langle E \rangle$ decreases due to more limiting water availability, and the maximum $\langle E \rangle$ allowed by the available water is attained over a wider range of hydraulic trait combinations, suggesting that multiple strategies may yield comparable fitness (Feng *et al.*, 2017). In Figure 3b, $\langle E \rangle$ increases as the maximum stomatal conductance increases with respect to the maximum sapwood conductivity, suggesting that plants with higher water transport capacity use water more efficiently. Note that no trade-offs between transport capacity and resistance to cavitation are implemented in this version of the model, so there is no physiological disadvantage in using water more intensively, except the fact that soil moisture is depleted faster, leading to reduced canopy gas exchanges. As in Figure 3a, changes in rainfall patterns affect $\langle E \rangle$ and tend to decrease its sensitivity to hydraulic traits, except for plants with extremely low ratios of stomatal conductance over sapwood conductivity.

When the plant carbon balance is also coupled to transpiration and soil moisture dynamics, it becomes possible to assess which hydraulic trait combinations yield highest fitness in a stochastic environment (e.g., in terms of mean growth rate). For example, results from a similar stochastic model show that different leaf phenological strategies (which control seasonal fluctuations in the Huber Value) provide a competitive advantage depending on rainfall statistics (Vico et al., 2017). Drought-deciduous species are predicted to have a fitness advantage and be resistant to invasion when the wet seasons are short, whereas evergreen species are favoured by long wet seasons. At intermediate wet season lengths, however, evergreen species can invade drought-deciduous communities, because of their more efficient water use. It is useful to contrast this approach to the modelling of drought-deciduousness against the approach taken across the semi-deciduous tropics in one TB model (Xu *et al.*, 2016). The statistical approach presented here and in Vico et al. (2017) stresses hydraulic trait diversity and covariation among traits to facilitate understanding of the ecological strategies governing spatial patterns and dynamics of drought deciduousness. In the example of the TB model (Xu *et al.*, 2016), relationships are prescribed by an *a priori* covariance matrix linking the traits across a diversity of PFTs and predictions of forest seasonality are tested against remotely sensed observations of canopy greenness.

V. Water fluxes in terrestrial biosphere models and feedbacks to community dynamics

TB models are the *de facto* platform for incorporating an ever-increasing range of plant-climate interactions into global climate models, including plant hydraulics (Hickler et al. 2006; Bonan et al. 2014). These developments can help improve representations of moisture limitations to ecosystem fluxes (gross and net primary productivity; evapotranspiration rate), phenology (LAI) and likelihood of drought-induced mortality in the basic spatial units of a TB model, i.e., the pixels composing the spatial grid of the modelled terrestrial biosphere.

Some TB models (Weng et al. 2015; Fisher et al. 2015, 2018) have recently co-opted a demographic approach (Moorcroft et al., 2001) for modelling sub-grid heterogeneity, distinct from the classic 'big-leaf' approach. As the name suggests, big-leaf models treat the entire canopy as if it were a single big leaf, averaging plant traits as they vary both vertically and horizontally through the canopy before calculating fluxes. In contrast, "vegetation demographic models" (*sensu* Fisher et al. 2018; hereafter VDMs) calculate fluxes for each cohort (a group of similarly-sized individuals of the same PFT) before averaging to the canopy. The key distinction between these two approaches as they relate to the modelling of plant hydraulics lies in plant size. While big-leaf models can account for different PFTs, they must average traits of individuals of different sizes within a PFT before estimating fluxes. Because plant height is such a ubiquitous driver of whole-plant hydraulic function (Mencuccini, 2003; Savage *et al.*, 2010; Olson *et al.*, 2018), and plant hydraulic processes are nonlinear, the demographic approach opens up new possibilities for models seeking to capture these nonlinear size-dependent effects of drought (and moisture more generally) on ecosystems.

Within this demographic framework, capturing nonlinear size- and trait-dependent effects of drought is accomplished by incorporating individual-scale plant hydraulic processes following the approaches outlined in Section *Main components of plant water transport models*. Such hydraulically-enabled VDMs (hereafter 'hydro-VDMs'), while in a nascent stage, are particularly attractive because they possess the capability of modelling hydraulic *trait-mediated environmental filtering*, in which climate 'filters' out PFTs in either spatial or temporal gradients of climate, based on their hydraulic traits. The previous section emphasized how ecosystem-level *fluxes* (but not vegetation dynamics) might change in response to hydraulic traits and shifts in the statistical properties of climate in space or time (see Figs 2 and 3). Here we highlight how hydro-VDMs can be used in the opposite direction, forecasting shifts in ecosystem-level hydraulic *trait distributions* in space and time, which in turn modulate ecosystem response to further climatic change.

Hydraulic filters operate at short timescales at the individual scale, VDMs handle the propagation

The working hypothesis expressed here (Figure 4) is that plant hydraulic traits are key filters operating at short timescales at the individual scale, but, when integrated over time or space, have long-term or large-scale consequences for ecosystem function. Hydro-VDMs are a useful tool to explore the long-term and large-scale consequences of these demographic feedbacks.

Consider two PFTs competing for space and resources in a grid cell. One PFT has a greater capacitance but a shallower root distribution, whereas the other has less capacitance but a deeper root distribution. In terms of growth and overall C gain, capacitance correlates with an enhanced ability to respond to high-frequency light variation (Meinzer *et al.*, 2008), hence, the competitive outcome between these two PFTs requires modelling the hourly timescale and integrating growth responses to annual timescales. The outcome is also contingent on the co-location of roots and favourable soil moisture in the soil profile. This is one among many possible contrasting trait combinations, in which competitive exclusion or coexistence can arise contingent on the outcome of processes affected by high frequency variation in environmental drivers (Powell *et al.*, 2018). A similar argument can be made that prediction of drought-induced mortality and seedling survival (Figure 4) have similar requirements of representing both short and long timescales. Hydro-VDMs translate fast-timescale processes into differential rates of resource acquisition and mortality among PFTs by 1) integrating fast-timescale net carbon gain to a daily timescale while tracking percent loss of conductivity (PLC) at the individual scale, 2) updating plant size respecting allometric constraints, 3) modelling resource acquisition as a function of plant size (tree height, leaf and crown area, rooting density and distribution), and mortality as a function of carbon and hydraulic status. Seed production is linked to individual carbon status and population density. Hence, growth, mortality, and recruitment all depend on the interaction between climate and hydraulic traits, generating a feedback between community composition and biospheric water fluxes.

The utility of explicitly representing the diversity of hydraulic traits across PFTs in a grid cell has been stressed before (Xu *et al.*, 2016). The challenge posed by this approach is in parameterizing these traits into a realistic yet tractable number of PFTs for simulations at large spatiotemporal scales. Defining what constitutes ‘realistic’ for the number and type of hydraulically-defined PFTs is fundamentally an ecological question (*sensu* Grime, 1979; Tilman, 1988), requiring delineation of both distinct drought survival strategies and the suites of plant traits which comprise them (e.g., Mursinna *et al.*, 2018; cf., discussion in Section *Main components of plant water transport models*). Going hand-in-hand with this challenge is the computational expense necessary to account for uncertainty in the degree of such trait coordination, often requiring ensemble simulations (Fisher *et al.*, 2010).

Natural experiments for evaluating models of trait-based filtering at large scales

Hydraulic trait filtering is the process hypothesized to be behind spatial patterns of species distributions across moisture gradients in Panama (Engelbrecht *et al.*, 2007), the Malay-Thai peninsula (Baltzer *et al.*, 2008), and at small spatial scales along the ridge-to-valley continuum in Amazonia (Oliveira *et al.*, 2018). While advances in incorporating trait diversity into VDMs have been made, approaches to date must prescribe trait diversity (Sakschewski *et al.*, 2016), rather than allowing it to emerge via simulated filtering. Quite possibly the most stringent benchmark for Hydro-VDMs is to predict the divergent hydraulic trait distributions in space in these ‘natural‘ experiments. Such spatial patterns may be used to estimate the potential impact of climate change on ecosystems, assuming space-for-time substitution is valid. At the global scale, we can contrast biomes in terms of their ‘reserve hydraulic diversity’ to accommodate climate shifts by recruiting new dominant hydraulic traits into the population. Ever-wet tropical biomes and low-diversity systems (e.g., boreal forests, some Mediterranean systems) may be particularly vulnerable to shifts in the statistical properties of environmental conditions (particularly, the return interval for mortality-inducing droughts). This high vulnerability emerges not necessarily because drought-induced mortality could be greater in these biomes, but because there is reduced likelihood for more drought-resistant taxa to preferentially recruit and become dominant because of the relatively constrained distributions of hydraulic traits exhibited in these systems. More diverse biomes have greater 'reserve hydraulic diversity' (e.g., seasonally evergreen and dry tropical forests, savannahs, some Mediterranean ecosystems, fynbos), and thus may be more resilient, consistent with recent findings demonstrating the role of community-level hydraulic trait diversity in buffering ecosystem drought sensitivity, albeit at short (daily) timescales (Anderegg *et al.*, 2018a).

VI. VI. Outstanding challenges in modelling water fluxes in the soil–plant–atmosphere continuum

1. Data availability versus model complexity

Ultimately, lack of sufficient high-quality data will remain the most important limiting factor for the adequate parameterization of water transport processes at large scales. Fundamental uncertainties on the occurrence and frequency of basic physiological processes (e.g., refilling) will continue to challenge modellers. Especially for TB models based on representing PFTs, representing the inherent variability of hydraulic strategies that are likely to occur within any one pixel will remain a challenge. Partly as a consequence of lack of data, it is also unclear how many axes of hydraulic variation should be represented in models, an issue that strongly constrains how models are structured. Work focussed on developing sound and easily applied hydraulic protocols remains a priority to remove a bottleneck for rapid data collection.

2. Scaling of tissue-level traits to the individual and the community

Some approaches (e.g., Bohrer *et al.*, 2005, Janott *et al.*, 2011) can resolve the differences in plant hydraulic architecture responsible for nonlinearities at the plant scale, but it is presently unclear how much detail is required to achieve consistent unbiased predictions at larger spatial scales. Details of fractal-like hydraulic architecture often need to be sacrificed to keep computational costs low (Mirfenderesgi *et al.*, 2016). While porous-media models have improved the realism of representation of hydraulics, the linkage of sapwood capacitance to the underlying traits via pressure-volume theory (turgor loss point, elastic modulus) has seldom been made (Christoffersen *et al.*, 2016). Phloem capacitance (Pfautsch *et al.*, 2015) is generally neglected in ecosystem and TB models, but phloem to xylem area ratios increase dramatically in twigs (Hölttä *et al.*, 2013). Because theory to interpret phloem diameter shrinkage is available (e.g., Mencuccini *et al.*, 2017), the assumption of negligible phloem capacitance should be revisited. The availability of global databases of sap flow (Poyatos *et al.*, 2016) provides opportunities to calculate *in-vivo* whole-system hydraulic properties using plant water potentials. Although this may appear as a step back to the use of 'apparent' pathway resistances/capacitances (e.g., Whitehead & Jarvis, 1981), the cross-checking of tissue-level traits and whole-plant traits may provide new avenues to investigate the robustness and generality of the tissue-to-plant scaling, the occurrence of potential bottlenecks in the pathway and whole-system vulnerability to environmental conditions or disturbance events. New empirical datasets of within-plant scaling of hydraulic properties (vulnerability curves, Huber values) will be valuable for hypothesis testing. Development of community-level distributions of hydraulic traits will shed light on the environmental and ecological controls of hydraulic trait distributions across diverse communities.

3. The memory of past drought events in the soil-plant continuum

At the root-soil interface, the traditional root shrinkage model (Herkelrath *et al.*, 1977) has recently been resuscitated thanks to a better understanding of the potential role of root hairs and root-derived mucilage with pectin-like behaviour (Carminati *et al.*, 2009; Carminati, 2012). In the plant xylem pathway, cavitation fatigue (Hacke *et al.*, 2001) contributes to building a memory of past droughts. The current debate on the likelihood of xylem refilling has renewed emphasis on the hydraulic significance of xylem growth. Tissue growth depends on turgor potential (Hsiao *et al.*, 1976) while growth produces new xylem conduits. Yet, the feedbacks between water status, xylem growth and its hydraulic consequences have not been examined (cf., Eller *et al.*, 2018b; Coussement *et al.*, 2018). Exploring the existence of trade-offs between plant hydraulics and xylem growth strategies will be a fruitful research and modelling avenue. Finally, distinguishing between evolutionary stable drought-deciduousness and defoliation leading to drought-induced mortality is already a major avenue for hydraulic modelling research.

4. Representation of non-xylary resistances in leaves and roots

The lack of leaf/root extra-xylary resistances remains a major weakness of current hydraulic models. This weakness is explained partly by the lack of extensive databases and partly by the limitations in our understanding of how certain leaf/root extra-xylary (e.g., apoplastic, symplastic, gaseous) pathways may respond to the environment. Leaf hydraulic vulnerability curves relate well to leaf turgor loss points (Nardini & Luglio, 2014) and a significant fraction of this increase in resistance during droughts occurs outside of the xylem (Scoffoni *et al.*, 2011; Sack *et al.*, 2016). Representing root/leaf extra-xylary conductance in models may provide a flexible way to include a greater proportion of total whole-plant resistance, give a better handling of the responses to severe drought past the point of turgor loss as well as include a relatively rapid stress recovery mechanism.

5. Links between hydraulic traits and other dimensions of whole-plant ecological strategies

Modelling of hydraulic transport must consider the integration of hydraulic traits within broader plant ecological spectra (Reich, 2014). Some models integrate water with light limitations (e.g., Sterck *et al.*, 2011; Mackay *et al.*, 2015), and many of the instantaneous stomatal optimality approaches mentioned above predict a direct coordination between diffusive conductances, photosynthetic capacity, xylem and/or phloem transport properties, consistent with much earlier literature. However, the integration of hydraulic traits within a broader trait framework still remains to be tested with a quantitative model, something more easily done when community-level trait PDFs are explicitly modelled across competing individuals (Christoffersen *et al.*, 2016). Similarly, very little work has been done to document how hydraulic properties jointly acclimate with other traits to long-term changes in environment (Domec *et al.*, 2017).

6. Thresholds for drought-induced mortality

There is currently a debate as to whether 'hard' hydraulic thresholds linked to mortality can be identified and what their values might be (e.g., Choat *et al.*, 2018). This discussion can be advanced by integrating mechanistic analyses of hydraulic failure with exploration of trait coordination and long-term xylem-phloem-canopy plasticity (Manzoni *et al.*, 2014; Mackay *et al.*, 2015; Mencuccini *et al.*, 2015). Some authors have proposed that conservation of cellular water content, in addition to plant water potential, may help define thresholds for mortality (e.g., discussion in Supplementary Data in Bartlett *et al.*, 2012). This avenue has merit in drawing attention to a complementary variable which may also scale with remote sensing products normalised within a daily cycle (Konings & Gentine, 2017). Expressing plant water status and fluxes in terms of both tissue water content and water potential is consistent with early modelling (Edwards *et al.*, 1986; Tyree, 1988) and current porous-media modelling.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1. Relationships among published Huber Values.

Table S1. Values of parameters used for Figure 3.

Notes S1. Details of analysis of published Huber Values.

Notes S2. Details and theory of ecosystem upscaling analysis.

Fig. 1 Synthesis of the conceptual scheme employed in this review. Plant hydraulic traits and properties drive water fluxes from soil to atmosphere at a range of spatio-temporal scales (a). Scaling of traits from one space-time scale to another depends on different sets of properties (b) and processes (c). (b) The scaling of traits from tissues to individual plants depends on a range of endogenous plant properties (from anatomy to allometry). The scaling from individuals to stands is determined by the community-level distribution of these hydraulic traits (community level mean and variance, i.e. diversity). Ecological (e.g. competition) and environmental (e.g. fertility, climate) factors affect how distributions of plant traits scale up to the stand. Finally, scaling from stand to grid cell averages is determined by the effects that hydraulic traits have on the long-term dynamics of stand development (recruitment, growth, competition, mortality). (c) The scaling of plant traits and properties is affected also by a number of processes. The scaling from tissues properties to individual plants depends on coordination among hydraulic traits (compensations, trade-offs). Plasticity and acclimation, the scaling of hydraulic traits vertically within canopies and site hydrologic balance affect the scaling from individuals to stands. Finally, environmental filtering of hydraulic plant functional type (PFT), trait distribution across land cover and PFT classes affect the scaling from stands to grid cells.

Fig. 2 Schematic representation of the four-step approach underlying most stochastic eco-hydrological models. (a) Relations between stomatal conductance (g_S) or xylem conductivity (k_X) and leaf water potential (ψ_L) are scaled up the stand level using leaf and sapwood area indices (LAI and SAI). (b) Stand level relations between transpiration rate (E) or net primary productivity (A) and soil moisture (s) obtained from the scaled-up properties from (a). (c) Soil moisture trajectory driven by stochastic rainfall events, resulting in the probability density function (PDF) of soil moisture ($p_s(s)$), which in turn determines the PDFs of E and A (respectively $p_E(E)$ and $p_A(A)$). (d) Because plant functional traits determine the shape of the transpiration and productivity response functions, the end result of these models (i.e. the probability density functions of water and C fluxes) depends on plant trait values in combination with the statistical properties of rainfall. Error bars indicate that the model outputs are stochastic, thereby fully characterizing the variability of E or A due to random rainfall events.

Fig. 3 Long-term mean transpiration rate $\langle E \rangle$ as a function of plant hydraulic traits, as predicted by a stochastic eco-hydrological model. (a) $\langle E \rangle$ as a function of the ratio between water potential at 50% stomatal closure ($\psi_{S,50}$) and water potential at 50% loss of xylem conductivity ($\psi_{X,50}$); (b) $\langle E \rangle$ as a function of the ratio between maximum stomatal conductance ($g_{S,max}$, expressed in mol m^{-2} s^{-1})) and saturated sapwood hydraulic conductivity ($k_{X,max}$, expressed in kg m^{-1} s^{-1} MPa)). In both panels, the ratios on the abscissa are varied by setting xylem properties (Supporting Information Table S1) and letting stomatal properties change. Line styles refer to different rainfall frequencies (increasing from dotted to solid curves, see key).

Fig. 4 Hydraulically-enabled vegetation demographic models and trait-mediated environmental filtering. Trait shifts occur via changes in the relative abundance of plant functional type (PFT) population densities, which in turn arise via the balance between recruitment (via seedling survival) and mortality. Overall growth and vigour are assumed to correlate with reproduction, which in turn sets the size of the seed bank for each PFT. The community trait distribution emerges from the relative abundance of multiple coexisting and competing PFTs, each characterized by plant traits and represented by a size distribution of cohorts (not illustrated for clarity). Bolded terms are hydraulic traits (non-exhaustive) governing the three demographic processes in relation to drought or moisture availability. Superscripts indicate sources demonstrating the trait effects. (1) Padilla *et al.* (2007); (2) O'Brien *et al.* (2014); (3) Johnson *et al.* (2018); (4) Anderegg *et al.* (2016); (5) Hoffmann *et al.* (2011); (6) Rowland *et al.* (2015); (7) Comas *et al.* (2013); (8) Meinzer *et al.* (2008). NSC-dep, storage/depletion of nonstructural carbohydrates; HSM, hydraulic safety margin between stomatal closure and occurrence of losses in xylem conductivity. (Adapted from Scheiter et al. 2011 for hydraulic traits; no permission required).

Model	**Optimization principle**	**Optimization criterion**	**Optimization conditions**	**Relevant temporal scale**	**Relevant spatial scale**	**Fitting parameters**
Cowan & Farquhar (1977)	Constrained maximization of gains	Max(A(g_s) - λ E(g_s))	$\frac{\partial A}{\partial g_s} = \lambda \frac{\partial E}{\partial g_s}$	Daily or longer	Stomata	λ
Manzoni *et al.* (2013)	Constrained maximization of gains	Max($\int_0^T A(g_s)\, dt$)	$\frac{\partial A}{\partial g_s} = \lambda \frac{\partial E}{\partial g_s}$ $\frac{d\lambda}{dt} = -\frac{\partial (A - \lambda E)}{\partial \theta}$	Daily to dry-down	Stomata and soil-root conductance (stand-scale)	None
Novick *et al.* (2016)	Constrained maximization of gains	Max(A(Ψ_L) - λ' E(Ψ_L))	$\frac{\frac{\partial A}{\partial g_s}}{\frac{\partial \Psi}{\partial g_s}} = \frac{\frac{\partial E}{\partial g_s}}{\frac{\partial \Psi}{\partial g_s}}$	Daily or longer	Stomata and xylem	λ'
Dewar *et al.* (2018): CAP model	Maximization of gains	Max(A(g_s, $V_{c,max}(\Psi_L)$))	$\frac{\partial A}{\partial g_s}$	Sub-daily to dry-down	Stomata and xylem (const. conductance)	None
Dewar *et al.* (2018): MES model	Maximization of gains	Max(A(g_s, $g_m(\Psi_L)$))	$\frac{\partial A}{\partial g_s}$	Sub-daily to dry-down	Stomata and xylem (const. conductance)	None
Prentice *et al.* (2014)	Minimisation of summed costs of two substrates	Min(E/A + $V_{c,max}$/A)	$\frac{c_i}{c_a} = \frac{\varepsilon}{\varepsilon + \sqrt{D}}$, $\varepsilon = \sqrt{\frac{b\ k}{1.6 a(\Psi)}}$	Months to years	Stomata and xylem	ε
Wolf *et al.* (2016); Anderegg *et al.* (2018b)	Maximum difference between gains and shadow costs	Max(A - Θ(Ψ_L))	$\frac{\frac{\partial A}{\partial g_s}}{\frac{\partial \Psi}{\partial g_s}} = \frac{\frac{\partial \Theta}{\partial g_s}}{\frac{\partial \Psi}{\partial g_s}}$, $\frac{\partial \Theta}{\partial \Psi} = a + b\Psi$	Instantaneous	Stomata and xylem	*a*, *b* of Θ(Ψ_L)
Sperry *et al.* (2017); Eller *et al.* (2018a)	Maximum difference between gains and hydraulic risk	Max(A' - Θ(Ψ_L))	$\frac{\partial A'}{\partial \Psi} = \frac{\partial \Theta}{\partial \Psi}$, $A' = \frac{A}{A_{max}}$, $\Theta = \frac{K}{K_{max}}$	Instantaneous	Stomata and xylem	None
Huang *et al.* (2018)	Maximum transport of assimilates away from loading phloem	Max($A^2(\Psi_L)$ - A(Ψ_L))	$\frac{\partial F_E}{\partial \Psi} = 0$	Daily or longer	Stomata, xylem and phloem	None

Table 1 Major types of models employing optimality criteria to predict stomatal conductance using hydraulic properties.

The table lists the optimization principle and criterion employed, the resulting optimization conditions, the temporal and spatial scales over which the optimality condition applies and whether or not empirical parameters need to be obtained by fitting the model against field data. The first model in the list (i.e. Cowan & Farquhar, 1977) does not include hydraulic traits, but it is given nonetheless because of its historical significance. A, photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; Θ, shadow cost function; Ψ_L, leaf water potential; A', relative photosynthetic rate; A_{max}, maximum photosynthesis at the point of critical water potential; K_{max}, maximum hydraulic conductance; F_E, export rate of sucrose from leaf phloem loading zone; c_i/c_a, ratio of intercellular to ambient CO_2 concentration; D, vapour pressure deficit; k, effective Michaelis-Menten constant for Rubisco; a, b, ε, λ, λ', fitting parameters; CAP, model accounting for reductions in carboxylation capacity ($V_{c,max}$) at low water potential; MES, model accounting for reduction of mesophyll conductance (g_m) at low water potential.

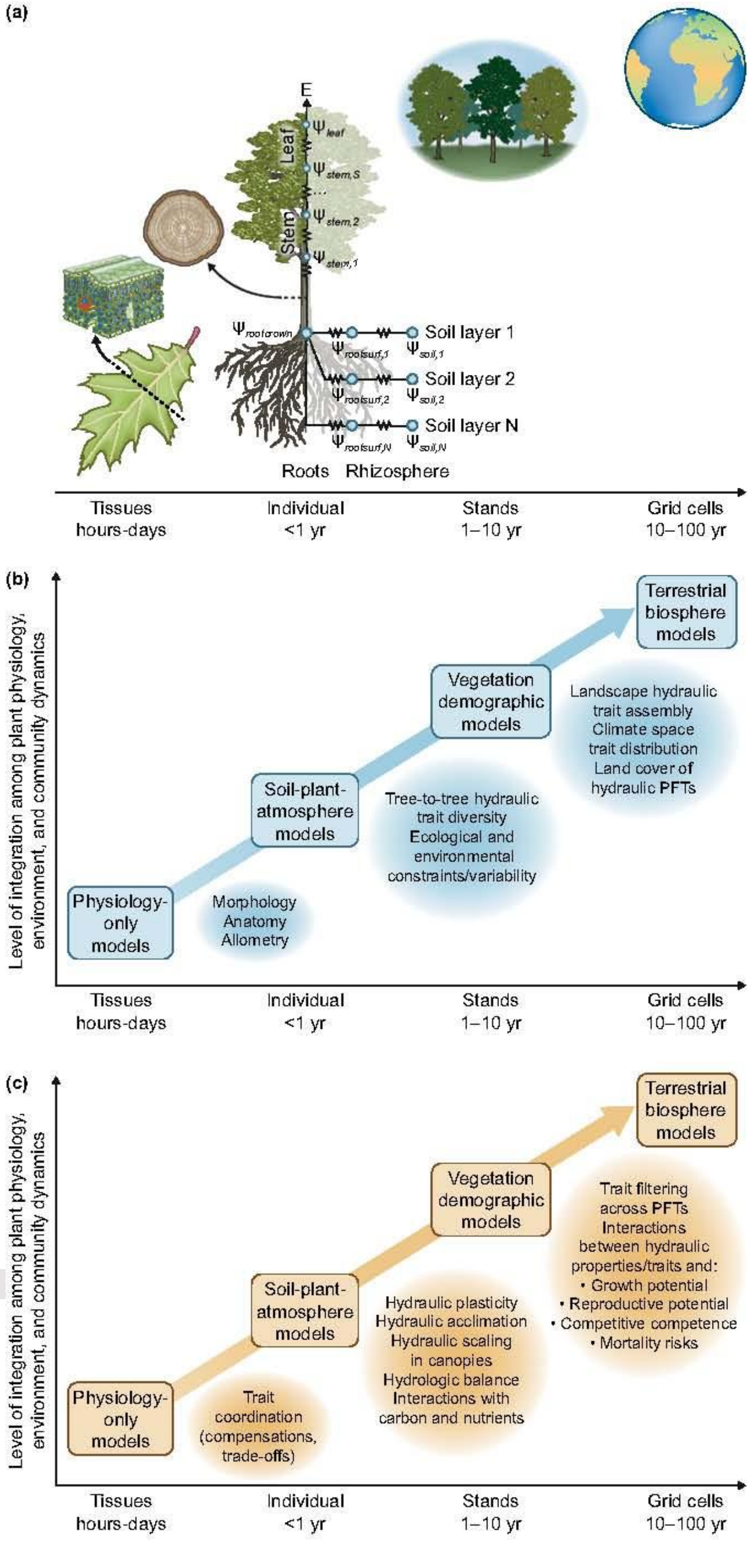
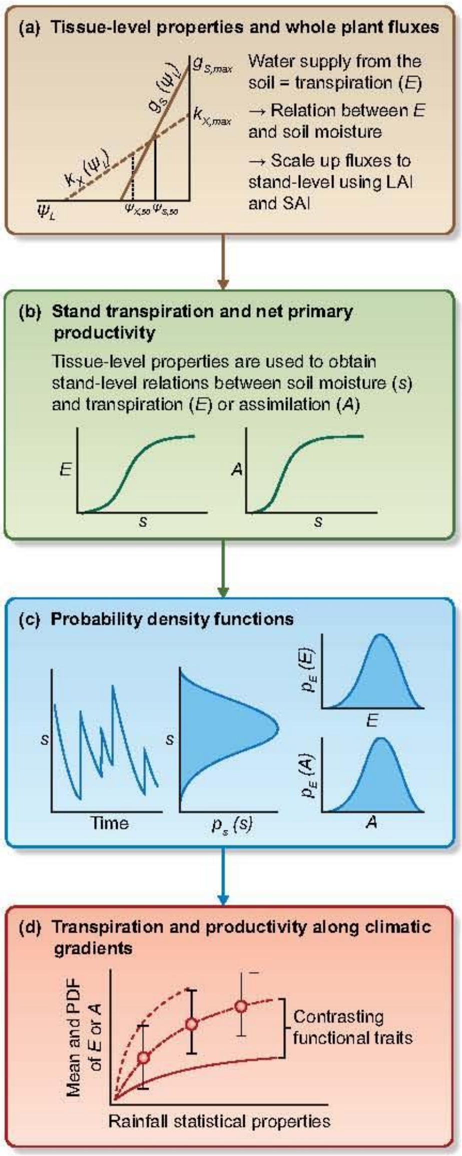


Figure 1

Tansley Review 27164



(a) Tissue-level properties and whole plant fluxes

Water supply from the soil = transpiration (*E*)

→ Relation between *E* and soil moisture

→ Scale up fluxes to stand-level using LAI and SAI

(b) Stand transpiration and net primary productivity

Tissue-level properties are used to obtain stand-level relations between soil moisture (*s*) and transpiration (*E*) or assimilation (*A*)

(c) Probability density functions

(d) Transpiration and productivity along climatic gradients

Figure 2

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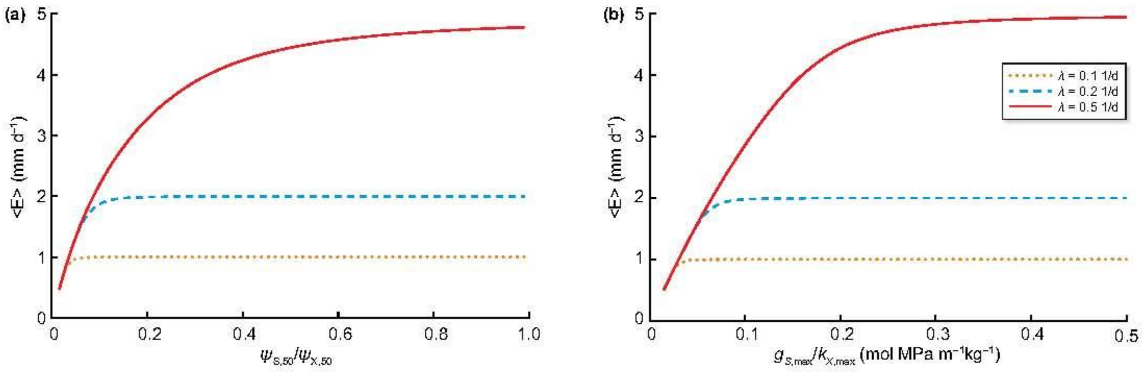

Figure 3

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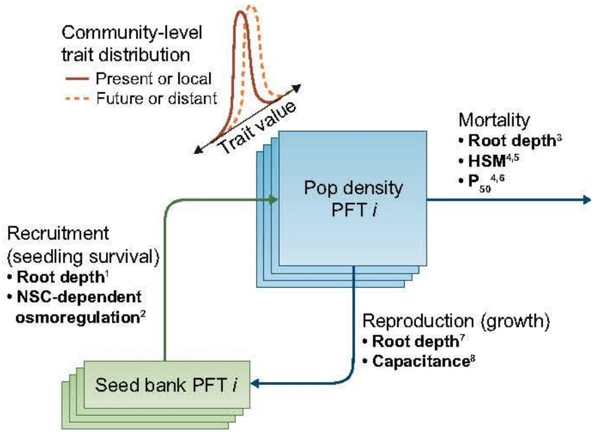

Figure 4

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