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SYMPOSIUM

The Ecosystem as Super-Organ/ism, Revisited: Scaling Hydraulics to Forests under Climate Change

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Synopsis Classic debates in community ecology focused on the complexities of considering an ecosystem as a super-organ or organism. New consideration of such perspectives could clarify mechanisms underlying the dynamics of forest carbon dioxide (CO_2) uptake and water vapor loss, important for predicting and managing the future of Earth's ecosystems and climate system. Here, we provide a rubric for considering ecosystem traits as aggregated, systemic, or emergent, i.e., representing the ecosystem as an aggregate of its individuals or as a metaphorical or literal super-organ or organism. We review recent approaches to scaling-up plant water relations (hydraulics) concepts developed for organs and organisms to enable and interpret measurements at ecosystem-level. We focus on three community-scale versions of water relations traits that have potential to provide mechanistic insight into climate change responses of forest CO_2 and H_2O gas exchange and productivity: leaf water potential (Ψ_{canopy}), pressure volume curves (eco-PV), and hydraulic conductance (K_{eco}). These analyses can reveal additional ecosystem-scale parameters analogous to those typically quantified for leaves or plants (e.g., wilting point and hydraulic vulnerability) that may act as thresholds in forest responses to drought, including growth cessation, mortality, and flammability. We unite these concepts in a novel framework to predict Ψ_{canopy} and its approaching of critical thresholds during drought, using measurements of K_{eco} and eco-PV curves. We thus delineate how the extension of water relations concepts from organ- and organism-scales can reveal the hydraulic constraints on the interaction of vegetation and climate and provide new mechanistic understanding and prediction of forest water use and productivity.

Introduction

Droughts are increasing in frequency and intensity under climate change, shifting species and forest distributions (Choat et al. 2018; Brodribb et al. 2020; Forzieri et al. 2022; Zhao and Dai 2022). Plant drought responses scale up to influence whole-ecosystem fluxes (Beer et al. 2010; Jung et al. 2017; Baldocchi 2020), which, in turn, affect how forests buffer atmospheric CO_2 accumulation and thus the rate of global warming (Keenan and Williams 2018; Harris et al. 2021; Sharma et al. 2023). Thus, understanding how the physiology of plant water transport ("hydraulics") scales up to whole forests is increasingly important.

Indeed, quantifying ecosystem hydraulic traits is a relatively new and timely research avenue. Given the need to predict resilience to climate change for diverse ecosystems—and, using even very coarse distinctions, there are >400 ecosystem types (Allen et al.

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Table 1. Scaling up concepts from organs to organisms to ecosystems or communities, emphasizing similarities and differences in processes across scales

Process	Organ (leaf, stem, or root)	Organism (plant)	Ecosystem/community
Development	Typically determinate (most leaves), or, in principle, indeterminate, but often environmentally constrained (stems and roots)	Typically indeterminate in principle, but often environmentally constrained	Growth/regeneration: typically indeterminate in principle, but often environmentally constrained Succession: once thought determinate (Clements), now indeterminate, given disturbance, climate change (Gleason)
Taxonomy	Simple based on botanical concepts, with some exceptions in particular lineages (e.g., Asparagaceae, Tiliaceae)	Simple, based on botanical concepts, with some exceptions, e.g., clonal plants	Complex to classify communities and ecosystems
Composition with respect to most salient units at lower scale	Cells and tissues within organs	Organs within plants	Complex to consider species and functional composition, given communities may be made up of characteristic species, or not, overlapping ranges
Metabolic/ transport rate/ flux rate estimation	Conceptually feasible to measure at organ scale	Conceptually feasible to measure or model from individual organ(s)	Complex: from Big Leaf and "Big Tree" to approaches that consider vertical (muti-layer) or horizontal (e.g., pixels across landscapes) heterogeneity

2015; He et al. 2019; Sayre et al. 2020)—extending well-developed organismal-based functional approaches to ecosystems would provide conceptual, measurement and inference tools to meet a critical need. Already, functional traits measured at ecosystem scale ("ecosystem traits") are increasing in utility, being analogous to species' functional traits and expressed as community weighted means per leaf area or per mass or per land area (He et al. 2019). Yet, establishing analogies from leaf- or plant-scale ecophysiologial concepts to apply directly to ecosystems, i.e., developing a "landscape ecophysiology," raises classic conceptual issues (Gleason 1926; Tansley 1935; Clements 1936; Roy et al. 2012). To what degree can a forest be understood as a single hydraulic system, responding to the soil and atmosphere?

Here, we review and reframe the classic "ecosystem as super-organism" debate and basic plant-water relations theory. We then review three applications of organ or organism concepts recently extrapolated in novel ways to the ecosystem scale: (1) canopy-scale leaf water potential (Ψ_{canopy}), (2) the ecosystem pressure–volume (eco-PV) curve, and (3) ecosystem hydraulic conductance (K_{eco}), within the context of the "ecosystem as super-organism" debate, as well as considering outstanding applications and research directions. Finally, we unite these new concepts in a novel framework to predict forest drought responses as they approach critical thresholds.

Revisiting the "ecosystem as super-organ/ism" debate

A classic debate focused on whether ecosystems or communities are predictable systems composed of species with similar or integrated environmental responses, and thus could be considered as "super-organisms" (Clements 1916, 1936). Alternatively, ecosystems may be composed of species with unique responses to environmental gradients such that no higher-level entity with predictable properties should be assumed (Cooper 1913; Gleason 1926). These historic debates tended to focus on both the strength of the analogy between ecosystems and organisms for specific processes (Table 1) and the more philosophical question of whether a community can act in its own interest, i.e., show a typical optimal behavior or "strategy," as one might expect for an integrated system such as an organ or organism (Gleason 1926; Tansley 1935).

There is currently a spectrum of comfort with approximating ecosystems as organs or organisms. Discomfort can be seen in functional trait theory, which carefully defines concepts as applicable only to individual organisms or species (Violle et al. 2007; Díaz et al. 2013), and in the noteworthy relative lack of exploration of ecosystem hydraulic concepts during the decades over which these ideas developed at leaf and plant scale. On the other end of the comfort spectrum are parsimonious "Big Leaf" models, routinely used to estimate global evaporation, productivity, and energy fluxes and their impacts on the coupled climate Earth system, representing the canopy as a single giant gas exchange surface (Raupach and Finnigan 1988). Further, comparative studies of ecosystems typically consider community-mean traits (weighted by the abundance of species; e.g., He et al. 2019; Liu et al. 2022, 2023; Chacón-Labella et al. 2023; Gomarasca et al. 2023), or, alternatively "ecosystem traits," such as maximum gross primary productivity (GPP), leaf area index, and leaf mass index, scaled per land area (Running et al. 2004; He et al. 2019). These formulations imply that ecosystem behavior can be related to its center of gravity with respect to its component species' traits. Indeed, some studies hint at a broader interpretation of ecosystems as like organs or organisms, with emergent behaviors as a "strategy" for the sustainability of their integrity and resources. For example, recent studies have explored the correlation among ecosystem-scale traits, using "strategy theory" previously developed at the scale of organs or plants (e.g., the "leaf economics spectrum"; Migliavacca et al. 2021; Gomarasca et al. 2023).

The development of broader scale approaches to measurements of ecosystems requires new frameworks for considering when we can model ecosystems as the sum of their parts, i.e., individuals of the same or different species or functional types, or as a single giant individual, behaving as a self-contained entity and thus, like an organ or organism. Here, we propose a simple rubric for distinguishing these "levels" when considering ecosystem-scale traits.

An ecosystem trait can be usefully considered as an "aggregated ecosystem trait" when scaled up from plant traits of component organisms, e.g., as a community species mean or community weighted mean. Aggregated ecosystem traits also include ecosystem properties or functions measured at larger scales and well understood theoretically as representing the simple aggregate behavior of component plant traits, such as the maximum ecosystem productivity derived from eddy-flux measurements and the fraction of absorbed photosynthetically active radiation derived from satellite products. We argue that an aggregated ecosystem trait is only tenable if it is stable and generalizable in principle for a given ecosystem in similar conditions, and/or across replicate ecosystems of given types (e.g., boreal forests, tropical lowland rainforests), and thus not susceptible to high variation arising from nonlinear dynamics of its component species, which would depend on the given context and timescale. For example, in still air, the ecosystem-scale leaf angle of a forest may meet the criterion of stability when averaged over a particular time interval, whereas under high wind, the ecosystem-scale leaf angle may not be predictable for that interval by scaling up from any scheme of sampling individual tree values.

A higher level of ecosystem trait, the "systemic ecosystem trait" represents a metaphorical super-organ/ism" trait, i.e., amenable to interpretation or prediction using concepts analogous to those developed for organs or organisms, thus implying optimization seen at ecosystem scale. Such concepts include, for example, the adaptation of traits to the environment or coordination or trade-offs among traits. Such systemic ecosystem traits would often be defined as parameters of functions fitted to ecosystem responses to environmental variables, such as the ecosystem-scale light-use efficiency (LUE). Notably, the trait remains a simple, scaled-up version of the traits of its component individuals, even though each individual tree trait value would be influenced by its micro-environment within the ecosystem. Thus, the systemic (metaphorical super-organ/ism) trait is simply a type of aggregated ecosystem trait, with a higher level of interpretation and prediction, implying optimality of behavior of the ecosystem as a whole.

Finally, a yet higher level of ecosystem trait, the "emergent ecosystem trait" represents the ecosystem as a literal super-organ/ism, with behavior influenced by the complex inter-relationships among component organisms, or, potentially, an apparent higher-level optimization in the ecosystem responses to the environment— even as the ecosystem changes composition during succession, assembly, or regeneration. Here too, the ecosystem trait remains an aggregated trait, i.e., representing a sum or average of the behavior of its component individuals. However, "emergent behavior" arises due to the distinct behaviors of its component species when they grow together compared to what is expected from simple aggregation of their properties as free-living organisms. For example, ecosystem-scale water use and water-use efficiency (or nitrogen use, and nitrogen-use efficiency) can be unpredictable from that of its individual species grown alone, due to interactions of their physiology when in competition drawing on the same soil water pool versus when there is differential access to water across the soil profile (Goulden and Bales 2019; El-Madany et al. 2021; Mas et al. 2024). Thus, the ecosystem as a whole might be best considered as a higher-level entity with its own behavior. The tragedy of the commons and ecological complementarity are two antithetic examples used to describe the behavior of ecosystems as literal super-organisms. While ecosystem behavior may be constrained by external environmental pressures on individuals, and the influences of individuals on each other, and not on a central, higher-level agency with self-awareness or power to create change to achieve a goal, the overall ecosystem behavior may yet be analyzed as if it were that of a literal super-organ/ism, optimized at a higher level to the environment and to its component mixture of species and functional types. This behavior is analogous to tissues within an organ, or organs within an organism, functioning toward an optimization of the performance of the whole. Indeed, if the various species within a sustainable community play specific roles, their interactions would likely contribute to the overall health and balance of the ecosystem. This idea might appear to conflict with the notion that competition for limited resources among species would overwhelm cooperative interactions. Yet, the hypothesis of niche differentiation and resource partitioning, often invoked to explain species coexistence, offers a possible explanation (Levine and HilleRisLambers 2009). For example, the assembly of shallow and deep-rooted plants reduces direct competition for resources and promotes coexistence, while potentially optimizing the resource use of the ecosystem, and thus contributing to its stability, resilience to environmental fluctuations, and sustainability (Eagleson 2005; Fargione and Tilman 2005; Kraft et al. 2015; Silvertown et al. 2015). Such complementarity would justify the consideration that forests function as a single system within certain contexts and timescales, behaving in a way that can be understood using simple metrics such as those typically applied to individual leaves or plants.

We note that distinguishing among levels of ecosystem traits (i.e., aggregated versus systemic versus emergent) is not always necessary in quantifying these properties, *per se*, or their relationships with other ecosystem traits, temporal dynamics, or spatial associations with environmental drivers. For example, when traits developed across species, such as the plant economics spectrum, are applied across ecosystems (Gomarasca et al. 2023), or when community-weighted mean ecosystem variables are related to climate across resource gradients (Muscarella and Uriarte 2016), these relationships may simply reflect the scaling up of the aggregated values of the component individuals and do not necessarily imply super-organ/ism behavior. However, when these relationships are interpreted based on optimality or eco-evolutionary theories developed for organs or organisms with these ecosystems treated as individuals, this implies a systemic (i.e., metaphorical super-organ/ism) behavior, and when specific relationships depend intrinsically on the community of coexisting species and their environmental responses, this would imply an emergent (literal super-organ/ism) behavior.

Thus, in developing ecosystem hydraulic traits, we advise consideration first of their usefulness as aggregated traits in terms of their generalizability and stability in given timescales and contexts, and second, whether these traits or their inter-relationships with other traits or with climate variables reveal optimization behaviors expected of organs or organisms, and third, whether there may be evidence of emergent behaviors suggesting ecosystems behaving as a whole. Finally, there is a need to consider additional complexities when calculating ecosystem hydraulic traits. One must decide whether to include the soil properties or simply the plants. Further, one must consider how to aggregate values for the plants, including which weighting factor applies to species (e.g., number of individuals, biomass, leaf area), and how to integrate over time. These calculations will impact estimates and our ability to validate or ground truth values, and need to be considered for specific contexts and applications.

Applying these concepts to develop and apply ecosystem-scale hydraulic traits will tap one of the greatest powers of plant physiology: to provide understanding at higher levels of biological organization by considering lower-level mechanisms and their potential transcendence (Passioura 1979). Hydraulic theory developed for organs and plants, if applied to ecosystems, could predict many of the features of the system using relatively simple empirical models and well-established physical principles (Raupach and Finnigan 1988). Further, if forests can be considered as self-contained entities with predictable hydraulic properties, heterogeneity within the forest may also be considered in this way, and likewise, larger-scale landscapes spanning multiple communities could be treated in the aggregate with weighted parameters.

Water relations theory

Water potential (Ψ) is the thermodynamic chemical potential of water, and with its components (pressure potential, Ψ_p, and solute potential, Ψ_s) can be used to quantify water availability and to analyze the driving forces for water movement (Jones 2014). Water potential can thus be defined for any medium (soil, plant organs, and atmosphere) and at any scale, and represents an index of its water status, correlated with its relative water content, where a lower water potential indicates a stronger ability to draw water from surrounding locations. The bulk water potential (Ψ_{leaf}) is often measured for equilibrated leaves, and represents the volume weighted average of the Ψ of its component cells. The Ψ_{leaf} measured at predawn—when the plant is presumed to be nearly equilibrated with the soil—is an important indicator of soil water potential (Ψ_{soil}), and thus community water stress, and can predict declines in ecosystem gas exchange and increasing tree mortality (Gu et al. 2015, 2016a, 2016b). The relationship between Ψ_{leaf} and relative water content is known as the pressure–volume (PV) curve and can be measured for different materials, e.g., wood, leaves, or soil (i.e., the soil moisture characteristic curve), and several key PV parameters provide insight into the behavior of the material. Thus, the leaf PV curve enables estimation of the leaf turgor-loss (or wilting) point, the threshold value of Ψ_{leaf} at which positive pressure (turgor) is lost.

Plant water movement occurs because water vapor diffuses from within the leaf across the leaf surface to the dry outside air. Copious water is lost when stomata open for CO_2 uptake, and, even after stomatal closure, plants continue to dehydrate due to water loss across the cuticle and from leaky stomata. Leaf dehydration reduces Ψ_{leaf} below Ψ_{soil}, creating a water potential difference ($\Delta\Psi$) that drives water flow from the soil to leaves. The hydraulic conductance is a dynamic property that represents the efficiency of water movement across a pathway, defined as the rate of water flow through any given component of the soil-plant-atmosphere continuum (SPAC) (e.g., a root, stem, leaf, or a whole plant) divided by the $\Delta\Psi$ across that segment (Tyree and Zimmermann 2002). At steady-state, the transpiration rate (T) equals the negative product of plant hydraulic conductance (K_{plant}) and the water potential difference between leaves and soil (Ψ_{leaf} - Ψ_{soil}):

$$T = -K_{\text{plant}} \times \left(\Psi_{\text{leaf}} - \Psi_{\text{soil}}\right). \tag{1}$$

And, rearranged,

$$\Psi_{\text{leaf}} = \Psi_{\text{soil}} - T/K_{\text{plant}}. \tag{1a}$$

During dehydration, the hydraulic conductances of organs and plants may decline due to aquaporin gating-induced reductions in membrane permeability in root and leaf cells, and eventually xylem embolism, which can block water transport i.e., "hydraulic vulnerability" (Verslues et al. 2023). Organ- and plant-level hydraulic conductances respond dynamically to temperature and irradiance (Henzler et al. 1999; Clarkson et al. 2000; Sack and Holbrook 2006; Scoffoni et al. 2008; Ben Baaziz et al. 2012). Plants generally prevent Ψ_{leaf} from falling below thresholds for turgor loss and catastrophic xylem embolism (Mencuccini 2003; Scoffoni et al. 2016), by investing resources to build conductive tissues, closing stomata as Ψ_{leaf} declines during soil and atmospheric drought, and accumulating osmotic solutes, which enable turgor to be sustained at lower Ψ_{leaf}. Thus, among species within given communities, $\Psi_{\text{leaf}} - \Psi_{\text{soil}}$ tends to be conserved, with gas exchange coordinated with hydraulic conductances diurnally and seasonally (Mencuccini 2003; Franks 2004, 2007; Martínez-Vilalta et al. 2014; Scoffoni et al. 2016; Sperry et al. 2016).

Canopy water potential

To fulfill a longstanding need for improving predictions of forest vulnerability to drought stress and fire, there is increasing interest in estimating Ψ at the community scale and beyond, integrating for pixels of forest canopy, community, or landscape (Table 2; Fig. 1; Konings et al. 2021).

Just as leaf-scale Ψ may be measured not only directly (e.g., with a pressure chamber or psychrometer; Rodriguez-Dominguez et al. 2022), but indirectly, using spectroscopic approaches (reviewed in Browne et al. 2020), Ψ can be mapped at canopy scale (Ψ_{canopy}) using empirical correlations with thermal and/or hyperspectral imagery from ground or airborne sensors, an approach well established in agriculture (e.g., dos Fernández-Novales et al. 2021; Santos et al. 2023). Remote sensing also provides avenues for making forest-scale measurements of Ψ_{leaf}, whether using proximal sensors, such as instruments placed on a tower above a canopy, or airborne sensors, or spaceborne sensors, such as, e.g., ECOSTRESS on the International Space Station (Schimel et al. 2019; Wong et al. 2023). Typical approaches include hyperspectral measurements (e.g., Rodriguez et al. 2011; Wang et al. 2020), microwave measurements of Earth's graybody radiation in the case of radiometry, or active radar signals (e.g., Konings et al. 2019, 2021) (Table 2).

Hyperspectral measurements enable relatively high spatial resolution measurements compared to microwave radiometry and, to a lesser degree, microwave synthetic aperture radar. Thus, hyperspectral measurements have been used for Ψ_{canopy} estimation across a variety of species and sites (e.g., Stimson et al. 2005; Cotrozzi et al. 2017; Wong et al. 2023; Sapes et al. 2024). Whereas leaf-scale hyperspectral measurements are made using an instrumental light source (Burnett et al. 2021), canopy spectral measurements require sunlight, and thus are not possible at pre-dawn, a time at which measurements of Ψ_{canopy} would provide an estimate of ecosystem-scale Ψ_{soil}. Because of their short wavelengths, hyperspectral measurements are only sensitive to the top-most leaves. By contrast, microwave measurements aggregate vertical variations in Ψ_{leaf} throughout most of the canopy, are not sensitive to clouds, and can be made at nighttime (Jackson and Schmugge 1991). The deeper area integrated by microwave measurements provides more meaningful information about Ψ_{canopy} fluctuations, but complicates interpretation and validation. Nevertheless, microwave radiometry measurements of Ψ_{canopy} can be made using tower-based (Holtzman et al. 2021; Jagdhuber et al. 2021) and space-borne (Momen et al. 2017; van Emmerik et al. 2017) sensors. Furthermore, microwave

Table 2. Compilation of some of the studies that paired remotely sensed products to leaf water potential or that modeled leaf water potential at canopy scale along with predictions of landscape-atmosphere fluxes

Type	Approach	Scale	References
Remote sensing			
Hyperspectral remote sensing	Defined hyperspectral index of water stress with leaf water potential	Community	Penuelas et al. (1993), Stimson et al. (2005)
Microwave remote sensing	Linearized relationship between water potential and tower or drone based observations	Community	Sepulcre-Cantó et al. (2006), Holtzman et al. (2021), Jagdhuber et al. 2021
Microwave remote sensing	Linearized relationship between water potential and satellite observations	Ecosystem	Momen et al. (2017), van Emmerik et al. (2017)
Thermal remote sensing	Defined multispectral index of water stress with leaf water potential	Community	Egea et al. (2017)
Terahertz remote sensing	Measurements of water potential and in-situ measurements scaled from leaves to across individuals and species	Intra- and Interspecific	Browne et al. (2023)
Remote sensing data assimilation			
Hyperspectral statistical modeling	Fitting multiple regressions to measurements of water potential and remote sensing products	Community	Rapaport et al. (2015), Cotrozzi et al. (2017), Sapes et al. (2022), Wong et al. (2023)
Model-data fusion	Model parameterized with location specific traits and remote sensing	Community/ Landscape	Binks et al. (2023), Holtzman et al. (2023)
Model-data fusion	Model parameterized with location specific traits and remote sensing	Ecosystem	Zhang et al. (2019), Liu et al. (2020)
Modelled			
CliMA Land	Stand-alone hydraulics	Community	Holtzman et al. (2023)
CliMA Land	Stand-alone hydraulics	Ecosystem	Wang et al. (2021), Wang et al. (2023)
Hydraulic Optimization Theory for Tree and Ecosystem Resilience (HOTTER) model	Stand-alone hydraulics	Ecosystem	Trugman et al. (2019a), Trugman et al. (2019b), Quetin et al. (2023)
CESM2 Community Land Model V 4.5 and V5	Hydraulics-enabled land surface model	Ecosystem	Bonan et al. (2014), Kennedy et al. (2019), Lawrence et al. (2019)
Ecosystem Demography model 2(ED2)	Stand-alone hydraulics	Ecosystem	Xu et al. (2016)
Terrestrial Regional Ecosystem Exchange Simulator (TREES)	Hydraulics-enabled land surface model	Community	Mackay et al. (2015)
Finite-difference Ecosystem-scale Tree Cr+A22own Hydrodynamics (FETCH2 and 3)	Hydraulics-enabled land surface model	Ecosystem	Mirfenderesgi et al. (2019), Silva et al. (2022)
Trait-driven forest model (TFSv.1Hydro)	Stand-alone hydraulics	Ecosystem	Christoffersen et al. (2016)
Noah-MP-Plant Hydraulics Scheme	Hydraulics-enabled land surface model	Ecosystem	Li et al. (2021)
Joint UK Land Environment Simulator (JULES-SOX)	Hydraulics-enabled land surface model	Ecosystem	Eller et al. (2020)
Community Atmosphere Biosphere Land Exchange	Hydraulics-enabled land surface model	Ecosystem	De Kauwe et al. (2020)

Plant hydraulic schemes are now available enabled in a number of stand-alone hydraulic models and as components of larger land surface models. These approaches can operate over canopies to entire ecosystems, and models can often be optimized with local water potential measures and remote sensing products or implemented for estimation when no in-situ measurements are available.

radiometry (Jackson and Schmugge 1991) and radar (Rao et al. 2019; Bernardino et al. 2024) can penetrate even dense canopies across a wide range of vegetation types and biomes (Bauer et al. 2019). However, tower-based microwave measurements remain customized and are not readily available, and space-borne measurements tend to have a relatively coarse resolution (e.g., 100 m or above for synthetic aperture radar and tens of kilometers for radiometry). The recent development of vegetation water content estimation from relatively cheap GPS sensors (Humphrey and Frankenberg 2023; Yao et al. 2024) is a promising new approach.

Overall, the application of these remote sensing tools to estimate forest Ψ_{canopy} is still nascent. Importantly, these are correlative tools, as there is no known direct biophysical wavelength response related to Ψ_{leaf}, but, rather, associations are based on the covariation of plant traits across time and space with water content (Wong

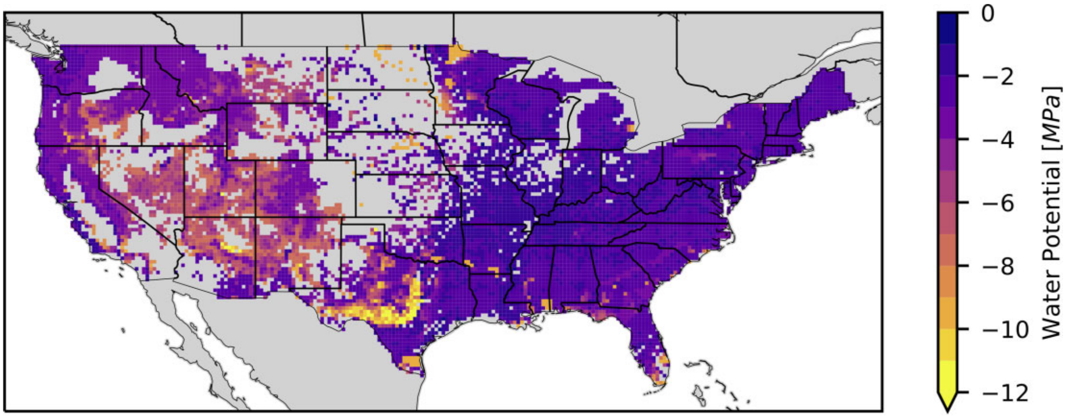

Fig. 1. Leaf water potential at tree canopy scale. The mean growing season (June 1st–August 31) leaf water potential modeled for the continental United States using HOTTER between 1995 and 2015 at 0.25 degree resolution. The color bar is skewed toward the less negative water potential values because those values are more representative of the majority of the pixels (Trugman et al. 2019b; Quetin et al. 2023).

2023). Indeed, one of the key challenges for remotely sensing Ψ_{canopy} is the need to account for spatial variations in the Ψ_{canopy} versus water content relationship, i.e., the ecosystem PV curve (eco-PV; Konings et al. 2019). This includes questions about scaling across individuals (e.g., whether the community-weighted mean Ψ_{leaf} or other measures should be used) and the role of other canopy properties (e.g., leaf angle and density, canopy sparseness, the presence of attached dead leaves in the canopy, and other branch properties). Gaps in our understanding of eco-PV relationships inhibit algorithm development, validation efforts, and answering questions about what larger-scale remote sensing of Ψ_{leaf} represents. For progress, we need a major increase in Ψ_{leaf} measurements across a diverse range of sites (Novick et al. 2022). The recent creation of the PsiNet network that is collecting existing Ψ_{leaf} observations into one database will likely be useful for such efforts (Restrepo Acevedo AM, Guo JS, Kannenberg SA, and Novick KA, in review).

Another approach to estimating Ψ_{canopy} is using models predicting land-atmosphere fluxes that have incorporated plant hydraulics. Plant hydraulics schemes are now enabled in a number of vegetation models, including tree-level models parameterized with observationally derived maps of species-specific or community weighted traits, such as the Hydraulic Optimization for Tree and Ecosystem Resilience (HOTTER) model (Trugman et al. 2019a, 2019b; Quetin et al. 2023) (Fig. 1), cohort-based ecosystem models that represent trees by size class, density, and plant functional type (PFT) (e.g., ED2-Hydro [Xu et al. 2016], FATES-Hydro [Christoffersen et al. 2016]), and the land surface components of Earth system models (e.g., in JULES [Eller et al. 2020], Noah-MP [Li et al. 2021], CliMA Land [Wang et al. 2023], LM3 [Cano et al. 2020], and CLM [Kennedy et al. 2019]), which use a modified Big Leaf approach to represent a handful of different PFTs across the globe. In the Big Leaf formulation, PFT biomass is aggregated by climate grid cell, often at ∼1 degree resolution (corresponding to ∼110 km on each grid side at the equator). In these models, within-community variations in species or plant water relations are generally not considered, particularly when run across large spatial scales. Thus, the simulated Ψ_{canopy} is "effective," but its scaling is not well understood (Anderegg et al. 2018; Browne et al. 2023). When plant hydraulic models are sufficiently computationally cheap, they can be used in combination with remotely sensed water content to optimize local PV curve parameters, allowing for estimation of Ψ_{canopy} informed by both data and models, even when no in-situ observations or prior information about local ecosystem PV curves are available (Liu et al. 2021; Holtzman et al. 2023).

Overall, the behavior of Ψ_{canopy} as an aggregated ecosystem trait requires further understanding to determine when it can be reconciled with measured Ψ_{leaf} values for trees and how stable it remains over important timescales (e.g., sunny periods, or daily or seasonal intervals). New studies are needed with ample Ψ_{leaf} data throughout the forest, and adequate ancillary data for leaf angles and leaf area indices, to determine whether estimates of Ψ_{canopy} can reasonably represent water potential averaged across a forest's leaves at a range of timescales, and in turn the degree this represents the water status of the ecosystem during drought and recovery. If so, Ψ_{canopy} will have obvious importance as an indicator of canopy water stress. Further, considering Ψ_{canopy} under particular conditions (e.g., daily maximum and minimum), Ψ_{canopy} may be useful as a predictor of whole forest gas exchange and productivity, and may signal the ecosystem approaching thresholds

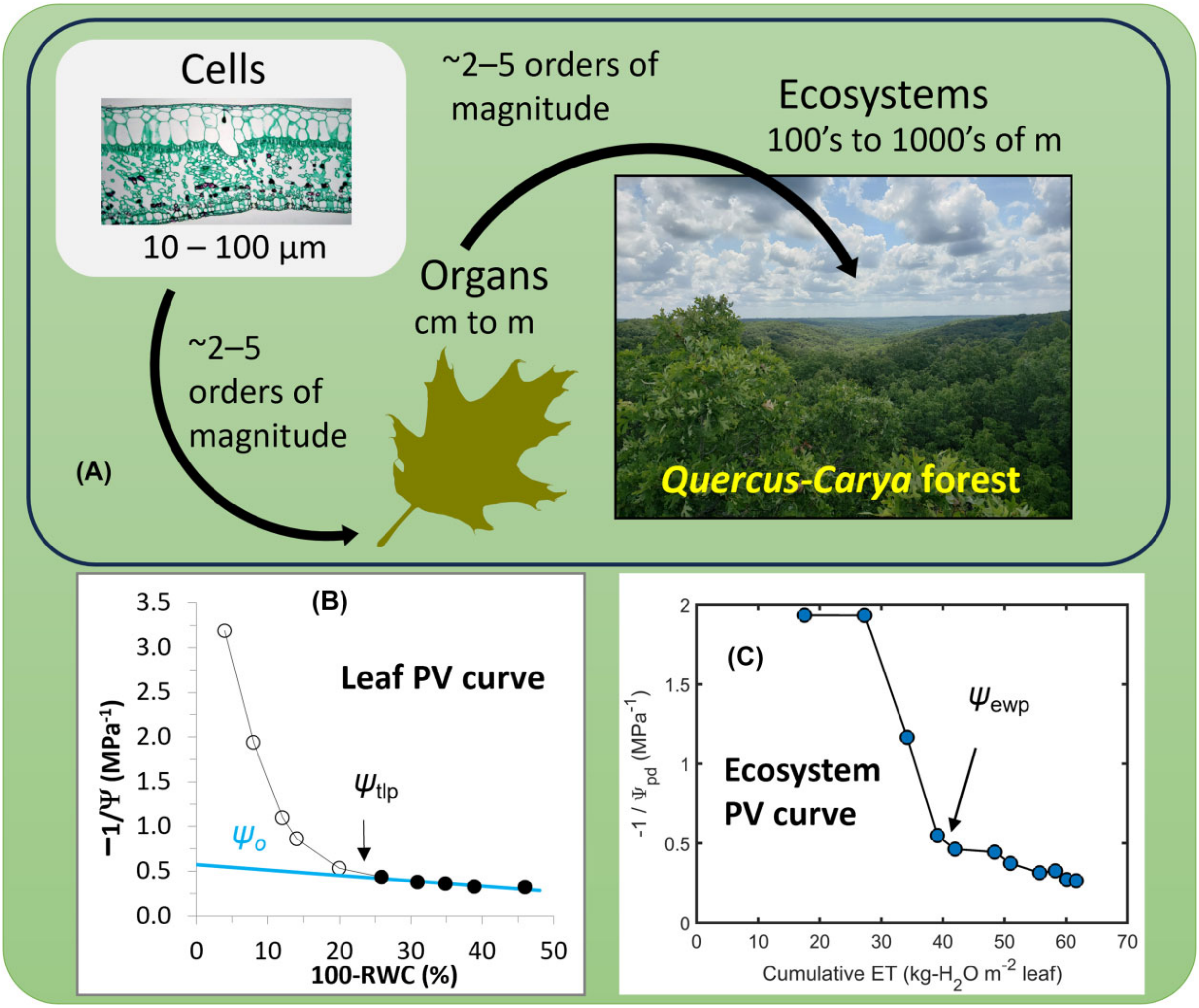

Fig. 2. The ecosystem PV curve. (A) The scale-jumps from cells-to-organs and organs-to-ecosystems are of similar orders of magnitudes; (B) PV curves used to analyze leaves were scaled up from cellular water relations theory, with (C) ecosystem PV curves taking it even further to describe plant community behavior. In leaf PV analysis, the water potential (Ψ) at turgor loss point (Ψ_{tlp}) is taken as the changepoint between linear and nonlinear segments. In the ecosystem PV analysis, defined using community predawn leaf Ψ (Ψ_{pd}), the ecosystem wilting point (Ψ_{ewp}) is taken as the changepoint between linear decreasing segments with steep and gentle slopes. The presented ecosystem PV curve represents overnight equilibration of water throughout the soil-vegetation system. RWC, relative water content; ET, evapotranspiration; Ψ_o, osmotic potential.

for stomatal closure, wilting, dysfunction, and potentially, flammability (Pascolini-Campbell et al. 2022). Future avenues for the study of Ψ_{canopy} include testing whether ecosystems regulate their transpiration rate to maintain Ψ_{canopy} above thresholds such as wilting point, as individual leaves and plants do, and whether this regulation shows emergent behavior that differs from that expected from scaled up scenarios based on component species.

Ecosystem PV curves

Water relations theory was initially developed at the level of cells and eventually was scaled up to consider tissues and organs in bulk, to derive plant traits such as the wilting point (Fig. 2; Tyree and Hammel 1972; Bartlett et al. 2012, 2014). Indeed, leaf-level PV parameters can be derived from the volume-weighted contribution of their cells' hydraulic properties (Tyree and Hammel 1972). At larger scales, an ecosystem pressure volume curve (eco-PV) could be used not only to calibrate remote sensing of water content to estimate Ψ_{canopy}, as described in the previous section, but also to estimate parameters such as the ecosystem wilting point (Ψ_{ewp}), with applications for predicting thresholds of forest responses (Wood et al. 2023).

Implicitly, "bottom-up" eco-PV curves are already calculated in ecosystem models that resolve the water potential gradients along the SPAC, based on the water content stored in the soil, xylem, and water storage tissues (Christoffersen et al. 2016; Lawrence et al. 2019; Li et al. 2021).

Recently, the eco-PV curve of a *Quercus-Carya* forest was constructed by plotting the negative reciprocal of community mean predawn Ψ_{leaf} against ecosystem evapotranspiration (ET) measured by eddy covariance (Fig. 2). This approach was developed by analogy to the leaf-level "bench-drying" method, in which dehydrating leaves are weighed to determine relative water content, along with determination of water potential (Richter 1978) and the "squeeze" method, in which cumulative water lost from leaves is weighed (Scholander et al. 1964), with the eco-PV curve "bulking" all plant cells and tissues and the volume of available soil water for the forest (Fig. 2A and B; Wood et al. 2023). Wood et al. (2023) conducted eco-PV analysis during a major drought with very low rainfall and used directly measured ET. In closed deciduous forest canopies, the growing season ratio of transpiration (T) to ET is usually >0.8 (Wilson et al. 2000; Wilson et al. 2001; Wehr et al. 2017), with lower ratios of ~ 0.7 possible immediately following rain (Wehr et al. 2017), making the use of measured ET appropriate for studying eco-PV curves. The derived Ψ_{ewp} represented an important functional threshold coordinated with carbon and water flux dynamics, as GPP decline corresponded to the timing of predawn leaf water potentials falling below Ψ_{ewp} (Fig. 2C)—at which point, the forest became insensitive to variations in environmental conditions. In the major drought year of 2012, community predawn Ψ_{leaf} was below the Ψ_{ewp} for nearly all of July and August, during which time the forest was a net source of CO_2. Notably, Wood et al. (2023) used absolute water content rather than relative water content as the x-axis variable of the eco-PV curve, which allows for Ψ_{ewp} estimation. However, the ability to determine other eco-PV parameters would require vegetation relative water content to be used as the explanatory variable, and that would likely require scaling up from the water relations properties of individual species.

Indeed, a separate study developed a "bottom-up" approach to estimating the eco-PV curve using relationships between aboveground plant water potentials and water content based on scaling up wood water retention properties under stable conditions (Binks et al. 2023). That study derived these curves at large scales across mixed canopies, and estimated other parameters such as ecosystem capacitance (Binks et al. 2023).

Finally, studies have directly estimated a key eco-PV curve parameter—the Ψ_{ewp} at canopy scale—using correlative remote sensing (Ordway et al. 2022; Vinod et al. 2022) or by mapping leaf turgor-loss point to the pixel, using a weighted mean for trees of component species within a grid cell, an approach applied in various contexts, i.e., along a topographic or aridity gradient within forest plots, or across large geographic areas (Bartlett et al. 2016; Kunert et al. 2021; Tordoni et al. 2022).

Eco-PV curves exemplify the context-dependence of an aggregated ecosystem trait. The eco-PV curve can be most effectively constructed for a forest at equilibrium with its soil, and, indeed, the Ψ_{ewp} determined this way was consistent with published values of leaf-level turgor loss points and with the moisture release characteristics of the soil (Wood et al. 2023). Yet, if one considers a transpiring canopy, the eco-PV curve may be too dynamic to provide generalizable or stable aggregate traits. Indeed, the Ψ_{canopy} would not show a single relationship with total water content, or relative water content, as it depends on the water potential gradients, hydraulic conductances, and water distribution within and across tissues and organs, which would change dynamically, nonlinearly, and possibly with hysteresis. Ultimately, for a transpiring forest, the multiple scales of inter- and intraspecific variation may lead to an extraordinary variation in the relationship between Ψ_{canopy} and water content under changing environmental conditions (Browne et al. 2023). Even in the case of eco-PV curves and parameters determined from pre-dawn values of Ψ_{canopy} and water content, studies are needed to determine how they represent the abundance-weighted distribution of a forest's component species' leaf and wood PV curves. Further, the potential insights provided by eco-PV parameters as potential super-organ/ism traits need consideration, i.e., exploration of how eco-PV parameters may be developed by analogy to the classic leaf PV analysis of traits that define plant drought responses [e.g., modulus of elasticity, osmotic potential at full hydration (Bartlett et al. 2012)]. Furthermore, tests are needed of whether eco-PV curve traits can be dynamic over seasonal timescales, in ways analogous to leaves or whole plants e.g., when plants use osmotic adjustment to maintain stomatal opening during drought (Bartlett et al. 2014). Future work must also consider variation across landscapes (i.e., pixels), determine the relationships of eco-PV curves with macro- and micro-climate, and assess whether ecosystem traits show deviation from those expected from their component species alone, indicating potential optimization or emergent behavior at the ecosystem scale.

Ecosystem hydraulic conductance

Leaf and plant hydraulic conductance are key traits that explain variation within and across species in environmental adaptation. Typically, plants with higher hydraulic conductance have higher rates of photosynthesis and water movement, and, declines in hydraulic conductance during drought presage or induce stomatal closure and plant mortality (Brodribb et al. 2007; Scoffoni et al. 2016; McCulloh et al. 2019; Beikircher et al. 2021). Thus, an extension of hydraulic conductance measurement to the ecosystem has strong potential to explain variation in carbon and water fluxes from plant to region under climate change.

The hydraulic conductance of the ecosystem (K_{eco}) can be defined as the bulk conductance (i.e., the root-to-leaf water transport efficiency) through the whole ecosystem expressed per leaf area or land area. K_{eco} has been considered using bottom-up approaches based on tree hydraulic conductances (Binks et al. 2022) and by inverting ecosystem model processes (Liu et al. 2020, 2021). Direct measurements may also be feasible, by combining eddy covariance measurements or remote sensing estimates of transpiration with on the ground Ψ_{leaf} measurements (Fig. 3). As a test of concept, we quantified K_{eco} for a Missouri *Quercus-Carya* forest. Assuming steady state flow through the soil-plant-atmospheric continuum, we defined K_{eco} (mmol m^{-2} leaf s^{-1}) as:

$$K_{\mathrm{eco}} = -T/\left(\Psi_{\mathrm{canopy,md}} - \Psi_{\mathrm{canopy,pd}}\right), \tag{2}$$

where T (mmol m^{-2} leaf s^{-1}) is canopy transpiration inferred from eddy covariance measurements using the TEA algorithm (Nelson et al. 2018), and $\Psi_{\mathrm{canopy,pd}}$ and $\Psi_{\mathrm{canopy,md}}$ are the weighted means (by basal area) of Ψ_{leaf} for component species measured at predawn and midday, respectively. Notably, T could also be estimated from remote sensing (Fisher et al. 2017; Melton et al. 2022). This conceptualization of K_{eco} constitutes a representation of the ecosystem as a "Big Tree," where, in theory, K_{eco} is equivalent to the sum of whole-plant conductances in the ecosystem, weighted by water potential differences, that is,

$$K_{\mathrm{eco}} \cong \sum \left[K_{\mathrm{plant},i} \times \left(\Delta\Psi_{\mathrm{plant},i}\right)\right]/\Delta\Psi_{\mathrm{eco}}, \tag{3}$$

where $K_{\mathrm{plant},\,i}$ and $\Delta\Psi_{\mathrm{plant},\,i}$ are the whole-plant conductance and leaf-soil water potential drop of the ith plant in the ecosystem, respectively, and $\Delta\Psi_{\mathrm{eco}}$is $\Psi_{\mathrm{canopy,\,md}} - \Psi_{\mathrm{canopy,\,pd}}$ (Fig. 3A).

Across dynamic environmental conditions over two growing seasons, the K_{eco} of this *Quercus-Carya* forest varied from 0.2 to 1.7 mmol m^{-2} leaf s^{-1} MPa^{-1}, and daily mean values showed significant positive relationships with irradiance and soil water potential. The feasibility of K_{eco} as an aggregate ecosystem trait was thus supported by its falling within the range of published K_{plant} values for tree species, including *Quercus* species in Missouri (Fig. 3C). While K_{eco} depends on the diversity of the trees in the forest and their micro-environments, the unified behavior of the system enables its consideration as an aggregated trait such that K_{eco} can be measured reliably. The concept of K_{eco} can be made tangible by estimating the diameter of pipe that would transport with the same efficiency as the trees of for one square meter of forest (Fig. 3B). Surprisingly, the pipe would be 0.5 mm in diameter, the typical thickness of the lead in a pencil! This small diameter illustrates the high resistance to flow through the vegetation, and how the internal plumbing bottleneck limits stomatal opening, and thereby T. Yet, vegetation achieves high flow rates and transpiration rates due to the high pressure-gradient driving force caused by low values of Ψ_{leaf}.

A full understanding of K_{eco} as an aggregated ecosystem trait depends on clarification of how it arises from its component trees. Just as variation across species in the partitioning of hydraulic resistances among organs can influence K_{plant} (Verslues et al. 2023), the K_{eco} would be determined by the conductances of its component trees and their organs. Further, the feasibility of K_{eco} as an aggregated ecosystem trait for use in comparative approaches requires testing in other forests that vary in species diversity and in spatial and temporal dynamics, to assess its generalizability and stability at given time scales. Considering K_{eco} as a systemic (metaphorical super-organ/ism) trait will enable testing of hydraulics concepts and theory developed at leaf and plant scales. One such avenue for future research is the hydraulic basis for ecosystem seasonal gas exchange dynamics. Does K_{eco} show high sensitivity to irradiance, and a steep vulnerability to declining soil water supply as do leaves, roots, and individual plants? A related question is the potential coordination of hydraulic supply and demand, and the potential correlation of K_{eco} with productivity across ecosystems, as found across leaves for diverse species (Brodribb et al. 2007; Scoffoni et al. 2016). Further, the hydraulic vulnerability of K_{eco} may be assessed, with parameters such as the Ψ_{canopy} at 50% or 80% loss in K_{eco}, and their potential trade-off with maximum K_{eco}, analogous to the safety-efficiency trade-offs often reported across species at organ-scale (Gleason et al. 2016; Scoffoni and Sack 2017). Indeed, by integrating knowledge gained from organ to ecosystem scaling, emerging remote sensing and modeling breakthroughs may be leveraged to enable mapping of ecosystem hydraulic vulnerability across the globe. Whether forests show emergent hydraulic behaviors that affect these trait-trait and trait-climate relationships remains to be tested.

Novel application: estimating leaf water potential and wilting from space

A crucial novel application of ecosystem hydraulics is utilizing eco-PV curves and K_{eco} for mechanistically based remote-sensing of Ψ_{canopy}.

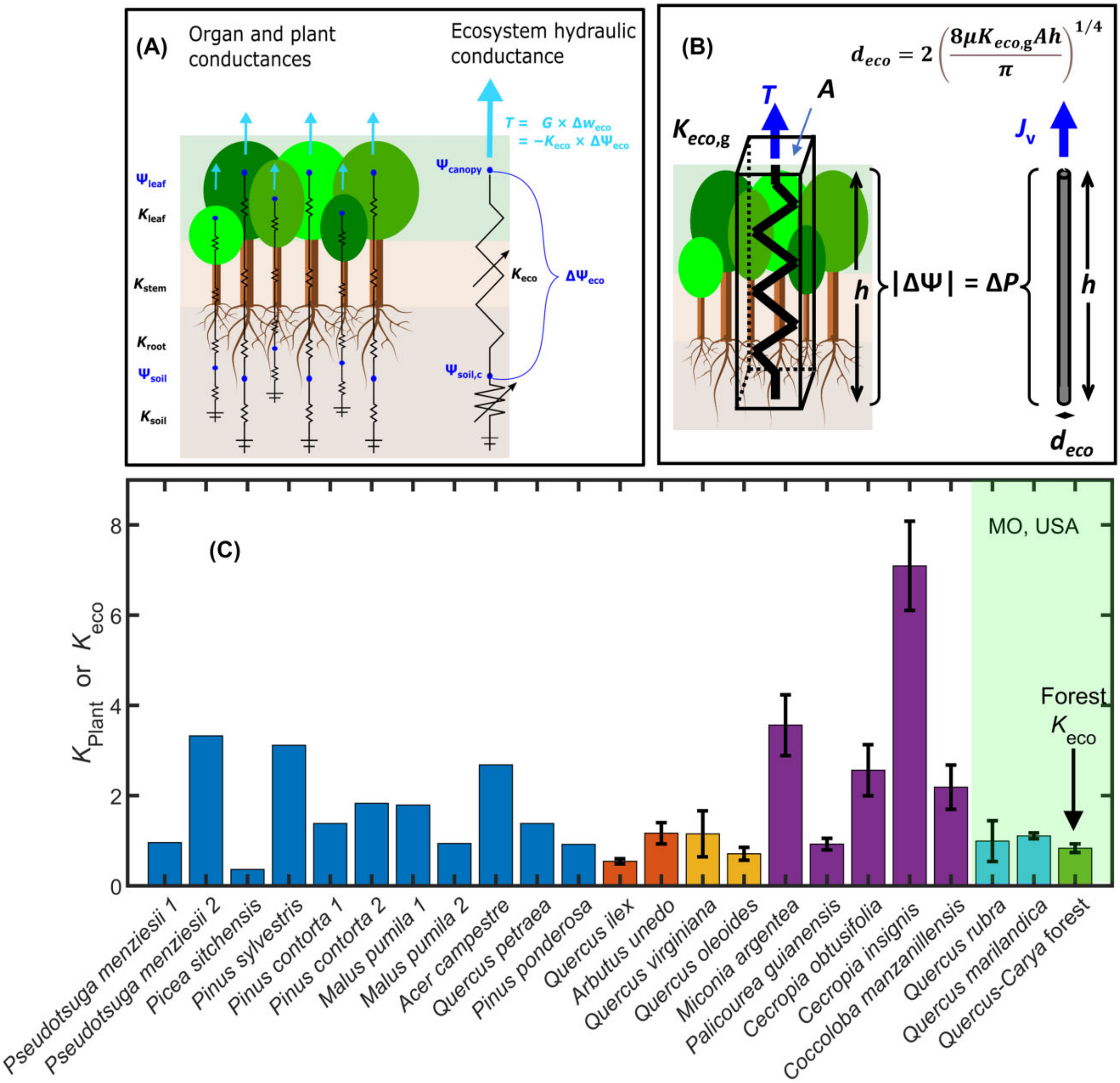

Fig. 3. Ecosystem hydraulic conductance. (A) Conceptual framework describing the ascent of water through an ecosystem and the ecosystem hydraulic conductance analog; (B) the "equivalent pipe" that represents the ecosystem conductance of a *Quercus-Carya* forest has a diameter of 0.5 mm; Starting from basic fluid dynamics and the Hagen–Poiseuille equation, we derived an expression for the diameter of an equivalent pipe (d_{eco}) that conducts a flow equal to forest-level transpiration and applied this for well-hydrated conditions with peak transpiration rates, $E = 10$ mmol m^{-2} ground s^{-1} and a typical water potential gradient of -1.5 MPa; (C) consistency of hydraulic conductances at the scale of whole-plants and ecosystems. In (C), the leaf-specific ecosystem hydraulic conductance (K_{eco}; units mmol m^{-2} leaf s^{-1} MPa^{-1}) of a *Quercus-Carya* forest, determined by combining eddy flux and water relations data (green bar) is compared to published data for leaf-specific whole-plant hydraulic conductances (K_{plant}; units mmol m^{-2} leaf s^{-1} MPa^{-1}) represented by blue bars for individual plants (Mencuccini 2002), while the others (red: Mereu et al. 2009; yellow: Cavender-Bares et al. 2007, purple: Meinzer et al. 1995, cyan: Reich and Hinckley 1989) are the means (± 1 standard error) of multiple individuals. The *Quercus-Carya* forest K_{eco} bar represents the mean (± 1 standard error) of 19 observations over 2 years. $K_{eco,g}$, ground area normalized ecosystem hydraulic conductance; T, ground area normalized ecosystem transpiration; h, canopy height; ψ, water potential; P, pressure; J_v, volumetric flow rate; K_{canopy}, hydraulic conductance of the canopy of leaves; $K_{stem,c}$, $K_{root,c}$, and $K_{soil,c}$ are the conductances of the stems, roots, and soil, respectively; G is the canopy diffusive conductance to water vapor; $\Delta\Psi_{eco}$, soil-canopy water potential difference for the ecosystem; d_{eco}, equivalent pipe diameter of the ecosystem; μ, dynamic viscosity; A, 1 m^2 area.

Using remotely sensed transpiration (T), previously measured K_{eco} as a function of its responses to environmental variables (x_n), and soil water potential derived from hydrological models, Ψ_{canopy} can be estimated based on an analogy to Equation (1a):

$$\Psi_{canopy} = \Psi_{soil} - \frac{T}{K_{eco}\,(x_n)}. \tag{4}$$

Notably, global mapping of T from space is now possible at daily time scales and at spatial resolutions better than 100 m (Fisher et al. 2017; Melton et al. 2022). The measurement relies on surface temperatures, meteorology, and vegetation greenness, which, when combined, constrain the radiative, atmospheric, and biological controls on evapotranspiration (ET; Fisher et al. 2008, 2011; Farella et al. 2022). Remotely sensed ET can be partitioned into canopy transpiration, soil evaporation, and interception evaporation (Miralles et al. 2016; Purdy et al. 2018; Talsma et al. 2018a, 2018b; Stoy et al. 2019; Sadeghi et al. 2020). The consideration of K_{eco} as a function of environmental drivers for the estimation of Ψ_{canopy} is analogous to approaches implemented for data driven model retrievals of GPP and the estimation of ecosystem LUE for remote sensing applications based on ecosystem-specific environmental response functions (Zhao et al. 2005; Bao et al. 2022; Xu et al. 2023).

Using such an approach, future work may be able to extract eco-PV parameters such as an Ψ_{ewp} from remotely sensed data, along with estimation of absolute or relative water content using scaling approaches, an ecosystem-scale analogy to the derivation of PV-curve parameters at leaf scale using spectroscopic approaches (Castillo-Argaez et al. 2024). A further potential application is to calculate pixel-specific ecosystem safety margins, analogous to those in leaves (Delzon and Cochard 2014), i.e., the difference between Ψ_{canopy} and the Ψ_{ewp} or the Ψ_{canopy} at 50% or 80% loss in K_{eco}, which may provide estimates of the vulnerability of communities to future climates, potentially beyond simply the vulnerabilities of its individual species. One may also quantify Ψ_{canopy} thresholds for wildfire spread and intensity (see Pascolini-Campbell et al. 2022).

Conclusions

Novel approaches to scaling up concepts developed for organs and organisms to ecosystems can provide apt tools to understand and predict ecological patterns across diverse environments. The idea of a community as an aggregate of individuals is sufficient to justify the calculation of ecosystem traits, and yet considering these traits further as representing ecosystems as super-organs or organisms enables the application of theory and approaches from leaf and plant to ecosystem scale, and the potential identification of the complex connections among the components that unite ecosystems into a single system with emergent behavior that can be understood and predicted. Applying these concepts, we can better constrain the control of fluxes, forest productivity, and ecosystem responses to climate change. Indeed, ecosystems show significant predictability in their hydraulic functions across climatic gradients (Migliavacca et al. 2021; Medeiros et al. 2023), suggesting a certain degree of coordination among their components, supporting the consideration of ecosystems across gradients by analogy to species biogeography (Liu et al. 2023). Yet, in certain contexts and timescales, ecosystem hydraulic traits may have limited value, if they lack generalizability or stability, as under some conditions the dynamics of a community may be more complex than those of a single organism, especially given strongly nonlinear, non-additive responses (Pacheco et al. 2021). Furthermore, climate change and other human-driven activities may sometimes disrupt the natural balance within ecosystems, leading to unpredictable responses for both the species and the community. Where an ecosystem sits on the gradient from aggregate of organs or trees to an integrated system to a higher-level emergent entity would thus depend on context, and a nuanced consideration is thus necessary as we continue to scale up approaches from organ to organism to ecosystem and beyond, toward improved conservation practices.

Author contributions

L.S. and J.W. led the writing of this paper with important contributions from all authors. Data analyses were conducted by M.B., A.K., G.Q., L.S., A.T., and J.W.

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Conflict of interest

The authors have no competing interest or conflict of interest to declare.

Data availability

Data underlying this article will be shared on reasonable request to the corresponding author.

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