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Opinion

A State Factor Model for Ecosystem Carbon–Water Relations

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With increasing calls for improving terrestrial carbon sequestration and sustainable water use, scientists are faced with the challenge of predicting changes in carbon–water relations from organisms to landscapes. We propose an integrative framework to help in answering basic and applied questions pertaining to coupled carbon–water functions in a variety of ecosystems. The conceptual framework is based on data from a globally representative set of ecosystems that hold vast amounts of carbon and provide water for rural and urban land uses. We focus on examples that demonstrate the value of an integrated approach that combines fast- and slow-changing state factors (i.e., variables that define structural properties and functional processes at the soil–plant–atmosphere interface) to improve predictions of carbon–water relations across scales.

Highlights

There is a growing need for land-use management and prioritization for optimal carbon gain and water conservation.

Interdisciplinary research will be necessary to better understand and improve the limits of carbon gain per water lost across scales.

A state factor approach inspired by soil and ecosystem science can be used to improve basic and applied knowledge of carbon–water relations.

A State Factor Model for Carbon–Water Relations

The study of carbon–water relations is central to the very notion of ecosystem functions and their essential services to society. Scientific understanding of carbon–water relations depends on our ability to quantify biophysical and ecological processes that control the exchange of mass and energy at the soil–plant–atmosphere (SPA) interface [1]. There is broad appreciation of the fact that changing species composition, ecosystem cover, and primary productivity as a result of both land use and climate change will affect both evapotranspiration (ET) and water yield (i.e., access to water resources) across ecosystems [2–5]. This leads to an important question: how might we simultaneously enhance carbon sequestration and improve sustainable water use locally, under global land use and climatic pressure? Public and private land-use sectors seek to scale up their carbon sequestration goals for climate mitigation [4]; however, the direction and magnitude of changes in water provisioning in response to management of carbon sequestration is uncertain, as are the impacts of rising carbon dioxide (CO_2) levels on vegetation cover and water lost through ET [2,6,7]. One key obstacle to policy and management efforts is the lack of a unified approach for scaling up coupled carbon–water relations from organisms to landscapes [8]. To address this limitation, we propose an ecosystem state factor model that integrates carbon and water provisioning as ecosystem functions which respond to a set of hierarchical variables that bridge different fields of inquiry.

Our proposal echoes calls for interdisciplinary integration to advance policy and management goals for enhanced carbon sequestration and water protection. It is based on a well-known trade-off between carbon and water fluxes that exists from leaves to ecosystems [9]. The limits of the carbon–water trade-off depend on both fast- and slow-moving state factors that define SPA interactions and resulting processes occurring above and below ground [8,10]. Accordingly, to garner a better understanding of how to link carbon–water relations, we build on the classic state factor model of soil development [11]. The core idea is that soil and ecosystem properties are a function of climate, organisms (i.e., plants, animals, microorganisms), topography, parent material (i.e., lithology), time, and disturbance. These state factors include dynamic biological

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processes as well as relatively stable geophysical and biophysical properties that must be looked at in conjunction if we are to improve basic understanding and applied knowledge of carbon–water relations. As in the state factor model for soil development, each of these factors acts independently on carbon–water relations, but must be integrated for quantitative prediction to account for local- and landscape-level processes in response to rising global climate variability. To improve understanding and applications, we consider relatively stable variables (parent material, time, and relief) in tandem with metrics of ecophysiological performance of dominant plant species (Table 1) that show how energy balance and pedogenesis influence carbon–water exchange above and below ground. This is possible because key slow-changing variables that can be easily measured across the landscape (e.g., topographic features derived from freely available global digital elevation datasets such as https://earthexplorer.usgs.gov/ can be used to constrain the limits of the carbon–water trade-off in plants, and further to understand patterns of belowground carbon storage [12]. This is exemplified by a simple standardization procedure (i.e., scaling data to units of 'standard deviations', with a mean of 0) that allows comparison of carbon–water functions across sites and landscapes relative to inputs and outputs compared

Table 1. Master Variables for Carbon–Water Relations, Their Temporal Stability, and Spatial Correlations[a]

State factor	Discipline	Variable	Temporal variability	Processes and feedbacks (Figure 3)
Parent material	Geology	Lithology	Slow	Soil weathering, soil carbon/nitrogen
Time		Age	Both	Mineralogy, base cation content
Relief	Landscape	Aspect	Slow	Sunlight, seasonality
		Slope	Slow	Infiltration, recharge, runoff
Response	Soil	Texture and depth	Slow	Soil moisture, soil carbon/nitrogen, recharge, runoff
		Mineral pH	Slow	Microbial community, nutrient availability, soil age
		C, C:N ratio	Slow	Water and nutrient retention, microbial immobilization versus mineralization of nutrients
		Microbial composition/activity	Dynamic	Nutrient acquisition and recycling
Organisms	Plant	Specific leaf area	Both	Competitive strategy, productivity
		Biomass (above/below)	Dynamic	Investment strategy, litterfall
		Seed mass	Dynamic	Reproductive strategy
		Diversity	Dynamic	Ecosystem resilience/plasticity
		Tissue stoichiometry	Both	Nutrient availability, photosynthetic capacity
Disturbance	Disturbance	Presence/absence	Dynamic	Past occurrence
		Recurrence Interval	Both	Probability of events, chronic versus discrete
Response	Ecosystem	Standing biomass/leaf area index (LAI)	Dynamic	Density, productivity, litterfall
		Productivity/normalized difference vegetation index (NDVI)	Dynamic	Productivity, litterfall
		Site index (dominant tree height: age ratio)	Slow	Potential productivity
		Evapotranspiration	Dynamic	Water loss and recharge
Climate	Climate	Temperature	Dynamic	Climate (and seasonality)
		Precipitation	Dynamic	Climate (and seasonality)
		Growing degree days	Slow	Life cycle
		Drought indices	Dynamic	Water stress

[a]Temporal stability is 'dynamic' if it is likely to undergo significant change within a seasonal timescale, otherwise it is designated 'slow'.

with a 1:1 line to assess the relative contributions of computed carbon drawdown and water use by plants and ecosystems (Figure 1).

Harnessing Trade-Offs in Carbon and Water Functions

Ecosystem carbon and water functions are inherently linked by potential gradients that span the SPA continuum and are driven by leaf–atmosphere vapor pressure differentials, that in turn control CO_2 diffusion and photosynthesis. Soil–plant interactions are important because it is not only the ability of the plant to pull, but also the nature of soil to resist (via capillary action), that governs the balance of carbon and water loss (or gain) between leaves and the atmosphere [10,13,14]. For example, intensive measurements of CO_2 and water vapor at relatively undisturbed locations that span some of the most productive ecosystems on Earth – evergreen conifer forests of the maritime North-Western USA – show that increasing air temperature and declining precipitation have recently brought those forests to 'the verge of switching from being carbon sinks to carbon sources' [13]. Crucially, the sensitivity of those ecosystems to climate depends on the ecophysiological performance of dominant trees, which is expected to vary with soil nutrients and water availability, as determined by dynamic biological processes, constrained by edaphic and

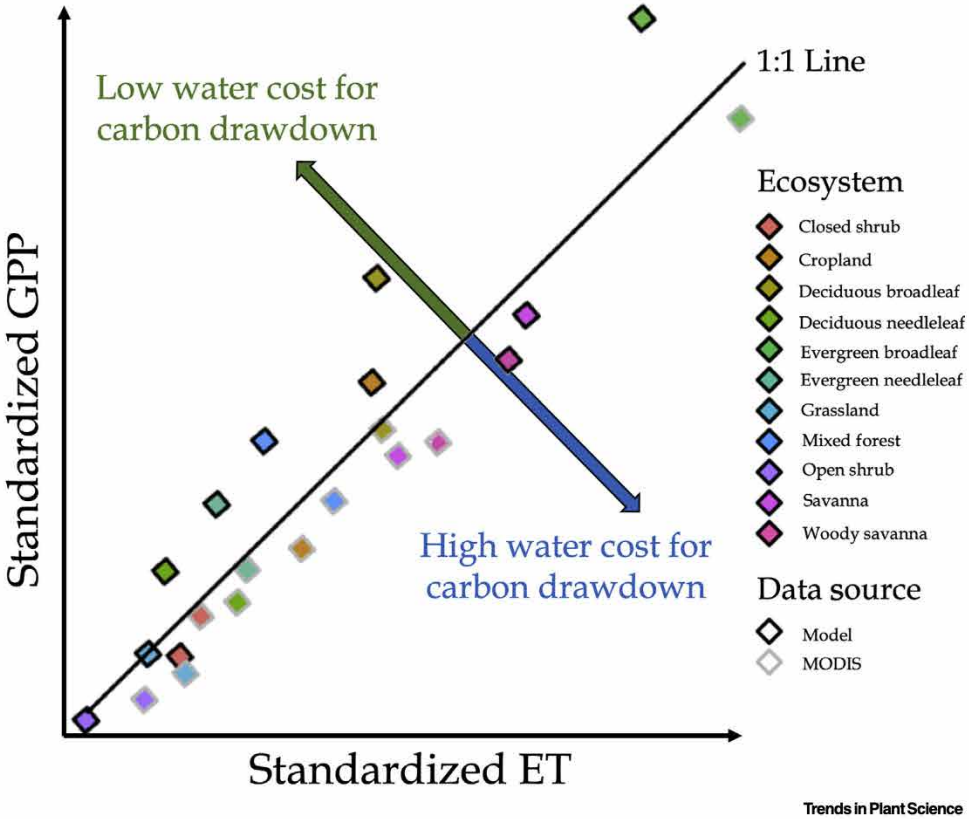

Figure 1. Conceptual Model Overlaid with Ecosystem-Scale Gross Primary Productivity (GPP) and Evapotranspiration (ET) from MODIS Satellite Data (Grey Outlines) and FLUXNET Eddy Covariance Data (Black Outlines) [16]. This illustrates a magnitude-independent trade-off between carbon gain and water use such that carbon sequestration is dependent on the amount of water transpired (which is often inversely related to water yields measured as streamflow [26]). Deviations from the 1:1 carbon–water line suggest that, despite this universal trade-off, carbon or water function might be maximized under some circumstances (Figure 2). In this conceptual scheme GPP and ET values are standardized to a mean of 0 and a standard deviation of 1.0 to allow comparison between the two variables regardless of unit differences. Points that depart from the line have greater value for provisioning of carbon or water, according to the direction (green and blue arrows) and proportionally to the distance from the line [6,36].

geographic landscape features. Evidence for this sensitivity at global scales is clear because major terrestrial biomes show varied responses to chronic environmental change (e.g., rising temperatures and atmospheric CO_2, shifting precipitation seasonality) as well as to discrete disturbance events (e.g., drought) [1,10,14,15]. This sensitivity is a reflection of the variation in a quasi-linear globally predictable gross primary productivity (GPP)/ET relationship (i.e., ecosystem water-use efficiency), which scales with plant cover from the least to the most productive biomes (i.e., dry shrub steppe to wet tropical broadleaf forests) [16]. This well-known relationship carries substantial variations in GPP (16–98%) and ET (16–83%) around the mean for different ecosystem types [16], which implies that the trade-off between carbon gain and water loss can be optimized at any given location. Indeed, long-term experiments have found that rising CO_2 levels can increase tree water-use efficiency and forest productivity depending on slow-changing soil physical and chemical properties [17]. Simply stated, the limits of the carbon–water trade-off from plants to landscapes are bounded by the amounts and overall availability of soil resources [18–21]. Thus, given the premise that, in the absence of resource limitation, ET and GPP will both scale with tree cover and productivity, a state factor framework provides a simple but meaningful way to interpret deviations from the average trend and harness biophysical and biogeochemical ecosystem properties for landscape prioritization aimed at optimal carbon gains and water conservation [1].

Carbon–water exchange at the SPA interface can be estimated by a variety of techniques, including leaf gas exchange, stable isotope discrimination, eddy covariance, and remote sensing. Importantly, the patterns of variation are not always consistent among these different types of data, where key discrepancies include differences between needleleaf and broadleaf trees and forests, and that isotope-based estimates of carbon–water exchange are higher than estimates based on ecosystem-scale eddy covariance [9,16]. It is not within the scope of this essay to discuss the merits and shortcomings of each approach, instead we discuss experimental and theoretical approaches that may enhance understanding of the varied drivers of these local- to global-scale metrics. As an example, we consider plant level water-use efficiency, or the ratio of carbon assimilated to water transpired, a semi-plastic trait – in other words it is more strongly controlled by inter- than intraspecific differences – which varies with landscape position and soil properties [9,22]. This assumption is supported by our recent analysis of nine dominant tree species across broad altitudinal gradient (~1500 m) covering a wide range of ecosystem types from mixed conifer to subalpine, and soil types from ultisols to entisols derived from three different lithologies in Northern California [22]. In this analysis, water-use efficiency was measured (via carbon isotope ratios of leaf cellulose) and combined with species traits, field-based surveys of soil properties, and both ground and remotely sensed metrics of stand productivity (i.e., leaf area index and normalized difference vegetation index; Table 1). The result was to show significant interactions between critical zone processes that proved useful in predicting changes in forest carbon–water relations over space and time. For example, changes in tree species composition were shown to have the potential to alter water-use efficiency at broad landscape scales owing to increases in water loss through transpiration (per unit of carbon fixed through photosynthesis) ranging from 10% to 60% depending on soil type. Looking ahead, we envisage applications of a hierarchical state factor approach to create land-use prioritization based on ecophysiological metrics and pedogenic thresholds to prescribe species mixtures that may increase carbon drawdown and maintain stream flow under changing climates.

Examples and Applications

Rising temperatures and CO_2 levels have been shown to shift the physiologically optimal climate zones of some tree species to higher altitudes and latitudes [23]. At the extremes of habitable montane terrain, for example, recent observations suggest that only half of forests display this

trend, and, given little ability to explain this disparity, researchers must employ a more holistic ecosystem approach (e.g., by considering lithology [24]) that addresses the impacts of global change on critical zone processes that control SPA interactions at local to landscape scales [25]. In the particular case of montane systems, the stakes are especially high because montane forests and meadows harbor most of the water that fills reservoirs and rivers for four billion people worldwide [5]. By some estimates, montane landscapes could see up to 26% decreases in river flow as a result of warming-induced increases in tree cover and ET [26]. Therefore, to simultaneously maximize carbon sequestration while maintaining water supplies, managers and legislators must consider a variety of factors that link local, manageable soil–plant factors (e.g., vegetation density) with broader environmental gradients. An example of how to do this is provided through an exploration of our state factor-inspired model that was developed to reflect the inherent link between GPP and ET (Figure 1). This model is applied here to a set of recent studies that quantified the productivity of forests under several different management scenarios (Figure 2A), and the efficiency/productivity relationships across broad environmental gradients (Figure 2B). The results show how ecological, pedogenic, and climatic data may be integrated to provide optimization of site function towards carbon or water provisioning.

In the first example, fertilizer additions and herbicide applications were combined across climatic, parent material, and topographic gradients in ponderosa pine plantations to assess the most

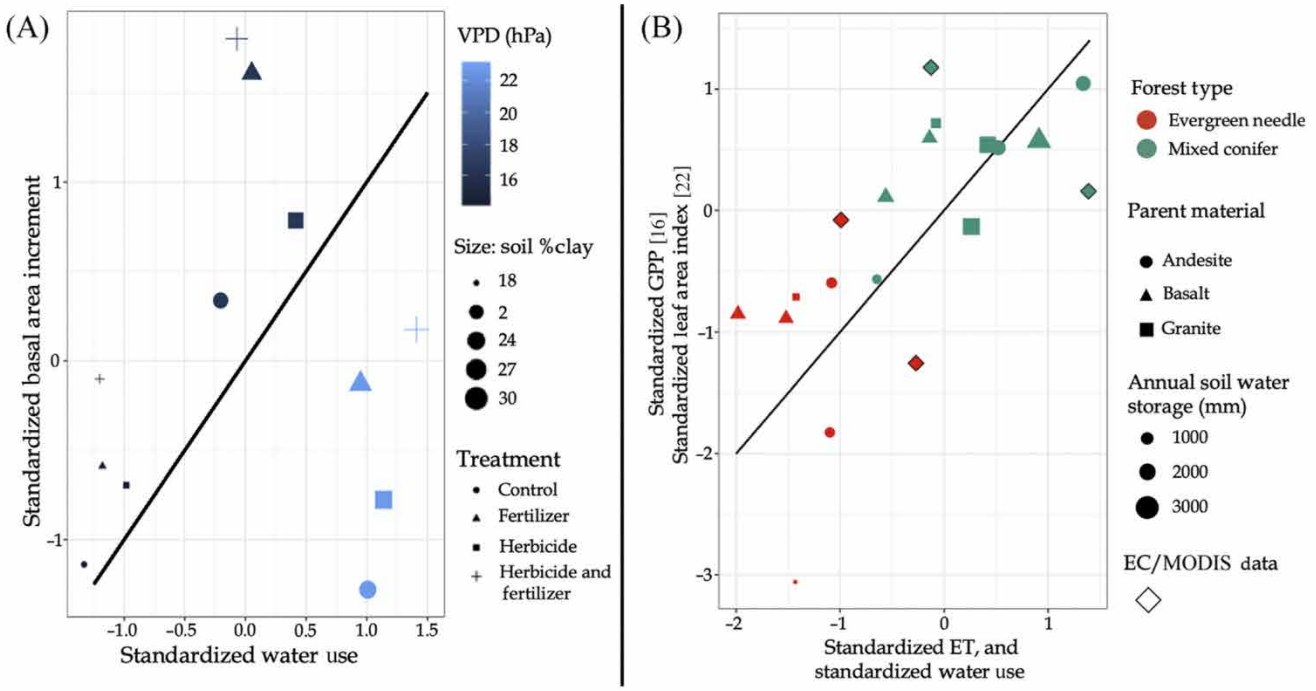

Figure 2. Applications of the Conceptual Model Proposed in Figure 1. In (A), datapoints represent standardized average tree growth and water-use values for a series of managed ponderosa pine forest plots across climatic gradients (colors) and soil textures (shape size) that affect site water storage. Experimental treatments (shapes) replicated across sites had significant effects on growth by limiting competition for soil resources, where high vapor pressure deficit (VPD) and coarse-texture soils have an equivalent impact on site productivity, but have distinct impacts on water use [17]. (B) Standardized data from two studies in unmanaged forests. First, MODIS satellite data and eddy covariance estimates (diamonds) represent globally averaged values for gross primary production (GPP) and evapotranspiration (ET) of two forest biomes (fill color) [16]. Other symbols represent ground-based measurements of GPP and ET derived from stand-level leaf area index paired with standardized water use from litter isotope data for nine dominant tree species in these biomes [22]. The data show significant deviations from the expected relationship between productivity and water use such that parent material (shape) and soil water storage (point size) determine the water costs of carbon gain across sites.

important factors driving tree and stand growth and water use. Site-level factors include those that represent productivity (i.e., average annual basal increment and canopy height) and an index for standardized water use as determined by the ratio between isotopically inferred intrinsic water-use efficiency and site vapor pressure deficit (VPD) [22,27]. The plot shows that low clay content and high VPD have a similar limiting effect on productivity and in explaining deviations from the expected 1:1 standardized carbon–water trade-off relationship. Deviations from the 1:1 line indicate proportionally greater water loss through ET for each unit of carbon gain at high VPD sites, whereas high clay and moderate VPD lead to high productivity and a proportionally greater carbon gain per unit of water used for transpiration (Figure 2A). Furthermore, in this example, experimental treatments replicated across sites strongly influenced the direction of carbon gain per water used, whereas soil texture and VPD exerted a stronger influence on water use than on carbon gain.

The second example uses leaf litter isotope data as an integrated metric of water-use efficiency across climatic gradients, varied forest types, and three contrasting lithologies. Water-use efficiency was scaled to the stand level by comparing stable carbon isotope data from standing litter and the associated leaf area index as an integrated measure of stand-level plant inputs [22]. For comparison, the standardized version of these data was plotted with MODIS (moderate resolution imaging spectroradiometer) satellite data (https://modis.gsfc.nasa.gov/data/) and eddy covariance tower data collected for similar systems at the ecosystem scale (Figure 2B), selected from the global carbon–water trade-off relationship (Figure 1). For simplicity, the MODIS

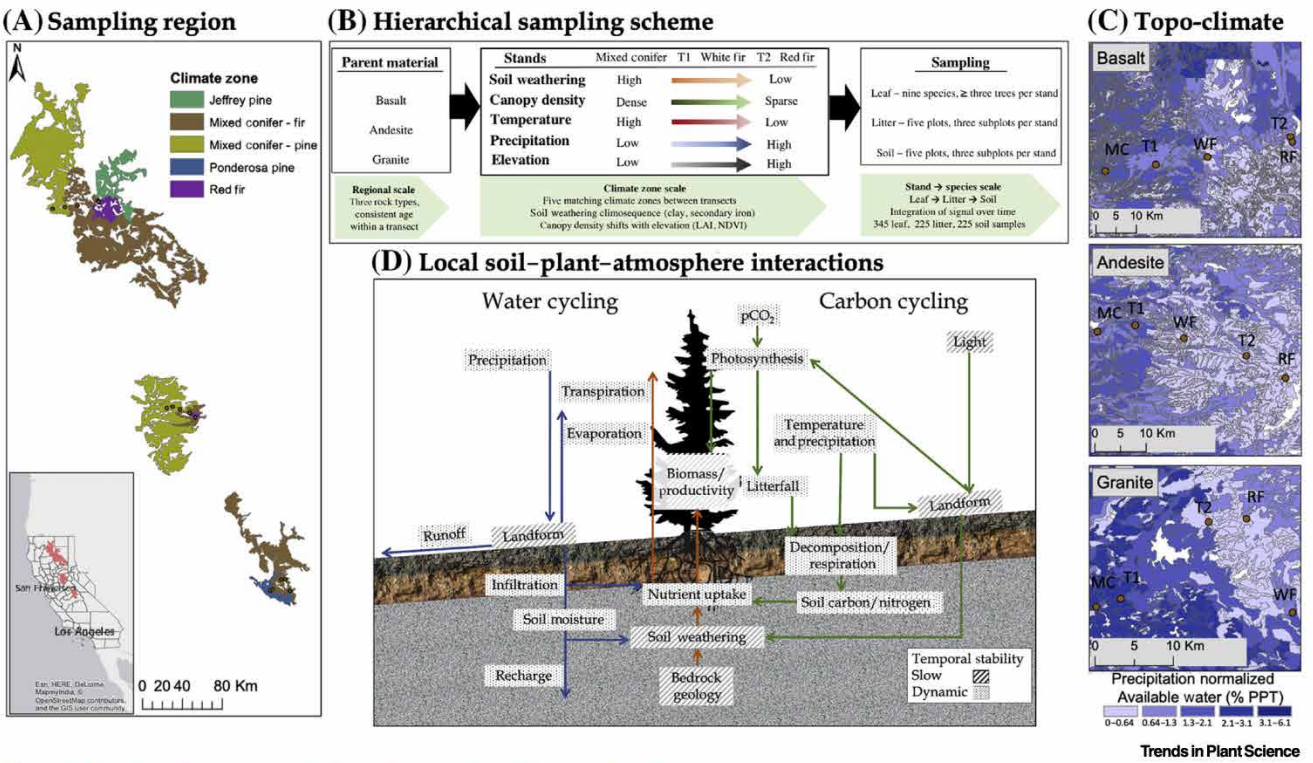

Figure 3. Sampling Strategy Used To Scale Carbon–Water Relations from Trees to Landscapes. (A) Example of a sampling region in Northern California where multiple forest types coexist across lithologies. (B) Proposed hierarchical sampling scheme [22]. (C) Topography and precipitation gradients across montane landscapes. (D) Local soil–plant–atmosphere interactions including above- and belowground processes that impact on carbon–water relations (e.g., water-use efficiency). Blue arrows are associated with altered hydrologic cycling, green arrows are associated with altered carbon cycling, and orange arrows are associated with processes that are subject to interactive effects between carbon and water cycles. Panels (A–C) are adapted, with permission, from Maxwell *et al.* [22] under CC BY-NC-ND 4.0. Abbreviations: LAI, leaf area index; NDVI, normalized difference vegetation index; PPT, precipitation.

data we used in this example represent only the relevant ecosystems represented by the litter isotope data, reflecting the same sites as those studied by Maxwell *et al.* [22], and have been colored to compare with data from the isotope-derived dataset. This standardized plot shows a clear relationship between GPP and ET regardless of the scale of measurement and the data used, as well as across ecosystems types and different forms of measurement. However, using size to represent soil water storage (a modeled value calculated from bedrock depth, soil type, elevation, topography, and climate [28]), we see that soil type governs the water cost of carbon gain across sites and ecosystems. Similar ecosystem types sampled across soils derived from basalt tend to have high carbon gain per unit of water lost through ET, whereas other parent materials (Figure 2B, shapes) were more often at or below the 1:1 carbon–water relationship. This demonstrates the basis for a state factor approach (detailed in Figure 3) that links site-specific measurements of soil–plant interactions and a series of master variables (Table 1) to quantify and scale coupled carbon–water functions in the context of optimized land use.

As in other biogeochemically diverse ecosystems, strong pedogenic and ecological gradients occur, giving way to a series of carbon–water trade-offs at different scales. We list a series of relevant metrics that can be measured from leaves to ecosystems that provide an efficient guide for sampling and observation (Table 1). A further aspect of our framework designates variables as dynamic (e.g., climate and ecophysiological processes) or slow-changing ecosystem conditions (e.g., soil properties or landform). Drawn from resilience theory, this assists in conceptualizing the susceptibility of an ecosystem to change [29,30]. For example, it is well known that species adapted to xeric environments tend to have high water-use efficiency and low productivity, but the geographic distribution of such drought-adapted species is expected to shift as (dynamic) seasonality tends towards greater extremes [31]. However, without considering gradients of (slow-changing) soil water-holding capacity (e.g., Figures 2B,3C), predictions of species migration and biogeographical rearrangements of plant communities cannot be perceived [21]. Moreover, although temperature will always influence photosynthetic CO_2 assimilation and plant transpiration at daily to seasonal timescales [32], it also exerts long-term effects over slow-changing ecosystem properties such as biogeographical patterns [33] and their influence on pedogenic energy and soil development [34]. For example, climate-induced stress on primary productivity and water loss through transpiration, both of which scale with tree cover [13], is expected to have a differential impact on the overlying ecosystem depending on the geologic substrate, and thus can be predicted on the basis of SPA interactions to illuminate the broad-scale changes that may occur [20]. Taken together, this framework provides a way to use landscape features to constrain carbon–water trade-offs across scales through accounting for differences in ecosystem structure and function to promote land-use optimization through an understanding of state factors that provide resilience to chronic disturbances (e.g., climate change).

Concluding Remarks

The ideas presented here respond to a need for increased awareness of scientific uncertainty that will be necessary to translate interdisciplinary science into policy and management to address the existencial concerns that our society is now facing (see Outstanding Questions). Indeed, the impact of policies that stimulate carbon sequestration and water availability varies greatly across a landscape even among similar ecosystem types [17]. This can hinder our ability to conserve or improve essential ecosystem functions. For example, maladaptive responses to environmental pressures can occur if the general public and policymakers 'miss the forest for the trees' in generalizing the application of a single management goal (e.g., carbon gain) at the expense of other essential ecosystem functions that may be better maintained in some portions of the landscape. For the specific example of carbon and water functions, a state factor framework provides a way to use well-known trade-offs in plant sciences so as to better prioritize landscape use. In addition

Outstanding Questions

How might plant and soil sciences be combined to push the limits of the carbon–water trade-off at scales that matter for climate change mitigation?

How might governance systems rely on quantitative analyses of SPA interactions to improve land use and reduce disturbance risks?

How does demand for carbon drawdown interact with resource limitation to shape socioecological trajectories in a changing world?

to carbon and water functions, SPA interactions are the target for empirical studies because they affect social and ecosystem stability as measured in provisioning services (e.g., vegetative productivity and water yields), regulatory services (e.g., carbon sequestration and groundwater recharge), as well as cultural, recreational, and aesthetic benefits [35]. In these areas we must better articulate the importance of cross-scale examination to enhance our ability to use relatable, manageable, metrics to inform regional resource management. Integration of knowledge from ecologists, geologists, geographers, and soil scientists can be combined into an actionable set of prescriptions for carbon sequestration and water conservation (Figures 1,2). This brings us to our original purpose: to promote a research framework that can uncover mechanisms that will aid in creating a mosaic of land-management strategies to operationalize known linkages between carbon sequestration and water yield across scales. A promising path forward would be to focus on emergent properties arising from productivity–efficiency relationships which are difficult to represent in isolation given the inherently dynamic or slow-changing nature of their constituents, but collectively may be well constrained based on a few basic properties (Table 1). The power of interdisciplinarity as a requirement for research on SPA interactions and applications is clear in this case because short-term observations in field trials for the selection of desirable plant varieties generate only a small insight into the multiple indirect effects of how the ecosystem functions. A more generalizable understanding often requires cross-scale thinking and integration of theories and methods to advance science and address societal needs.

Acknowledgments

The ideas and some of the data used in this study were generated through projects funded by the National Geographic Society's Committee for Research and Exploration (EC-422R-18), the US National Science Foundation (NSF) Convergence Accelerator Pilot 1939511, NSF Plant Biotic Interactions 1758947, and Atmospheric and Geospace Sciences 1602958 (to L.C.R.S.). We are thankful to two anonymous reviewers and members of the Soil–Plant–Atmosphere Research Laboratory at the University of Oregon for valuable comments and suggestions.

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