



One Metric, Many Meanings: Reconciling Water Use Efficiency Definitions

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Received: 3 June 2026 / Accepted: 17 September 2026
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Abstract

Purpose of Review Water Use Efficiency (WUE) is widely used to describe carbon–water coupling, but its meaning varies among disciplines, measurement approaches and spatial and temporal scales. We review commonly used WUE definitions and formulations and clarify their conceptual differences.

Recent Findings Ratio-based metrics, including WUE (A/E) and intrinsic WUE ($A/g_s w$), describe realized carbon–water exchange but remain sensitive to environmental conditions. Optimality-based approaches distinguish these ratios from the marginal water cost of carbon gain ($\partial E/\partial A$), providing a mechanistic perspective on water-use strategy. We also highlight differences among leaf, plant, ecosystem, isotope, and model-derived estimate.

Summary WUE is best understood as a context-dependent metric rather than a universal functional trait. We propose a framework linking each formulation to its carbon and water variables, spatial and temporal scale, environmental dependencies, and underlying assumptions. This approach supports transparent metric selection and improves comparisons across studies, scales, and methods.

Keywords Water use efficiency (WUE) · Intrinsic water use efficiency (i WUE) · Marginal water cost of carbon gain · Stomatal optimization · Functional traits · VPD · Ecosystem water use efficiency

Introduction

Water Use Efficiency (WUE) is widely used to characterize the relationship between carbon gain and water loss in vegetation, applied across a range of research contexts ranging from leaf-level physiological responses to ecosystem

carbon–water exchange. At the leaf scale, WUE can be calculated as the ratio of carbon assimilation to transpiration, whereas at the ecosystem scale it is commonly expressed as the ratio of gross primary productivity (GPP) to evapotranspiration (ET) or transpiration (T). These formulations provide useful information about carbon–water coupling, but they do not necessarily represent the same process or respond to environmental drivers in the same way [1–4].

The interpretation of WUE depends on how changes in its numerator and denominator arise: WUE can increase because carbon uptake increases, because water loss decreases, or because both fluxes change at different rates, each with different physiological meanings [4–6]. For example, under drought, stomatal closure can reduce transpiration more strongly than carbon assimilation, producing higher WUE without necessarily indicating greater productivity or improved drought tolerance [7]. Thus, a change in WUE is informative only when the processes underlying changes in carbon gain and water loss are considered.

The expansion of WUE across disciplines has produced a diverse set of operational definitions [8, 9]. At the leaf scale, gas-exchange measurements provide instantaneous

We encourage authors to adopt this nomenclature system to reduce ambiguity and improve cross-study comparability.

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estimates based on assimilation, transpiration, or stomatal conductance. Stable-isotope measurements provide temporally integrated estimates related to intrinsic WUE [2, 10, 11], whereas whole-plant measurements relate carbon gain or biomass production to water consumption over longer experimental periods. At the ecosystem scale, eddy covariance provides estimates based on carbon uptake and water-vapour fluxes, while remote sensing and process-based models extend WUE estimates across larger spatial and temporal domains [12–16]. Although these approaches address related aspects of carbon–water exchange, their estimates are not automatically equivalent because they differ in the processes, spatial domains, and temporal periods represented [17, 18].

At the leaf scale, carbon assimilation and water loss are coupled primarily through stomatal regulation, creating a fundamental trade-off between carbon gain and water expenditure ([10, 19, 20]. Two commonly used leaf-scale formulations capture different aspects of this trade-off: instantaneous WUE is expressed as $WUE = A/E$, whereas intrinsic WUE is commonly expressed as $\text{i}WUE = A/g_s w$, where A is net carbon assimilation, E is transpiration, and $g_s w$ is stomatal conductance to water vapour [1–3]. Under conventional assumptions, that stomatal conductance to CO_2 is related to $g_s w$ by the diffusivity ratio of 1.6, that cuticular CO_2 conductance is negligible, and that the CO_2 concentration gradient is approximated by $C_a - C_i$, $A/g_s w$ can be related to $(C_a - C_i)/1.6$. However, this relationship should not be treated as an identity independent of the gas-transport model. Lamour et al. [21] showed that incorporating cuticular conductance and a more complete representation of CO_2 and H_2O transport can alter the estimation of C_i and stomatal conductance, while measured A and total transpiration remain unchanged. Thus, $A/g_s w$ and $(C_a - C_i)/1.6$ should be regarded as equivalent only under the assumptions of the corresponding gas-exchange formulation [21, 22].

WUE incorporates realized transpiration and atmospheric demand, whereas $\text{i}WUE$ relates assimilation to stomatal conductance independently of VPD [23]. The interpretation of $\text{i}WUE$ derived from gas exchange additionally depends on the assumptions used to calculate stomatal and CO_2 conductance from measured gas fluxes [21, 22]. Neither formulation should be assumed to represent an environment-independent property of a plant [24, 25].

Recent work has emphasized that ratio-based formulations should be distinguished from measures intended to characterize underlying water-use strategy. Liang et al. [5] evaluated WUE (A/E), $\text{i}WUE$ ($A/g_s w$), and the marginal water cost of carbon gain, $\lambda = \partial E / \partial A$, and showed that these quantities capture different aspects of plant water use. Whereas WUE and $\text{i}WUE$ are ratios whose values can respond strongly to environmental variation, λ is derived from the

sensitivity of water loss and carbon gain to changes in stomatal conductance and provides a more mechanistic perspective on water-use strategy. Under the Cowan–Farquhar optimality framework, this quantity provides a mechanistic perspective that differs from instantaneous carbon-to-water ratios [5, 26, 27]. Bonan et al. [27] further demonstrated that alternative stomatal optimization objective functions, based on either $\text{i}WUE$ or WUE, can produce different responses of stomatal conductance and carbon assimilation to atmospheric demand and plant water status, confirming that the choice of WUE formulation encodes different hypotheses about how plants balance carbon gain against water loss [27, 28].

This distinction also raises the question of whether WUE should be considered a functional trait. Violle et al. [29] defined a functional trait as a measurable morphological, physiological, or phenological characteristic of an individual that can be characterized without reference to the environment. Many WUE formulations do not strictly meet this criterion because their values depend on environmental conditions, measurement scale, and temporal integration: $A/g_s w$ and A/E can vary in response to VPD, irradiance, temperature, atmospheric CO_2 concentration, and soil-water availability, even when the underlying plant strategy is unchanged [23, 24, 30]. We therefore use WUE primarily as a context-dependent process metric rather than assuming that it represents an environment-independent functional trait [5, 29].

Differences among WUE estimates can therefore arise even when measurements describe the same vegetation because the underlying carbon and water fluxes differ. Ecosystem WUE based on GPP/ET includes non-transpirational components of ET, such as soil evaporation and canopy interception, whereas GPP/T is more directly related to transpiration [14, 31]. Similarly, leaf $\text{i}WUE$ obtained from gas exchange represents conditions at the time of measurement, whereas isotope-derived estimates integrate physiological information over longer periods and depend on assumptions relating carbon isotope discrimination to the ratio of intercellular to atmospheric CO_2 concentration [2, 16, 32]. These metrics may therefore provide complementary rather than interchangeable information.

The central challenge is therefore not that WUE lacks a meaningful physiological basis, but that the same term is used for quantities that differ in their definition, process representation, spatial scale, temporal integration, environmental dependence, and intended application [33]. Such differences can undermine cross-study comparability, introduce interpretive ambiguity, and hinder our ability to scale plant responses to water availability from local experiments to ecosystem observations and global models [9, 24, 34, 35]. This challenge is particularly relevant under

Table 1 Overview and comparison of empirical, modelled, satellite-derived, and optimality-based definitions of WUE

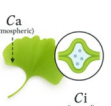
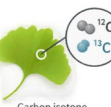
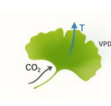
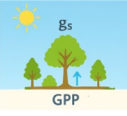
Type	Scale (Temporal scale)	Variable	Method	Harmonized Definition	Formula	Key assumptions and limitations	References
Empirical measurements	Leaf (Instantaneous / short-term)	 δ WUE – gas exchange	Leaf gas exchange (IRGA)	Ratio of net photosynthetic carbon assimilation to stomatal conductance to water vapour. It describes the carbon gained per unit stomatal water-conductance pathway under the conditions of measurement.	A/g_w	Strongly dependent on environmental conditions, including VPD, light and temperature. The relationship with $(C_a - C_i)/1.6$ relies on conventional diffusion assumptions for the stomatal pathway.	(7,15,16,21,23,24,29,40–52)
	Leaf (Seasonal to annual / tissue formation period)	 δ WUE – isotope-derive	Carbon isotope discrimination	δ WUE inferred from carbon isotope discrimination through its relationship with C_i/C_a . It integrates physiological information over the period represented by the sampled tissue rather than providing an instantaneous gas-exchange value.	$A/g_w = (C_a - C_i)/1.6$	Integrates physiological information over the period represented by the sampled tissue. Requires assumptions linking isotope discrimination to C_i/C_a ; not directly equivalent to instantaneous gas-exchange δ WUE	(4,8,9,42–44)
	Leaf (Instantaneous to short-term)	 δ WUE _{VPD}	Leaf gas exchange (IRGA) + VPD normalization	δ WUE normalized by atmospheric VPD to reduce the influence of atmospheric evaporative demand on comparisons among measurements. $k = 0.5$ where a square-root normalization is adopted.	$(A/g_w) / VPD^k$	Depends on the normalization function/exponent used. VPD normalization does not remove environmental dependence or make δ WUE universally comparable across environments.	(21,33)
	Leaf (Instantaneous to short-term)	 WUE _{leaf}	Leaf gas exchange IRGA	Ratio of net C assimilation (A) to leaf transpiration (T) measured at leaf scale	A/T	Directly reflects instantaneous leaf carbon–water exchange but is strongly influenced by VPD and other environmental conditions. Not equivalent to δ WUE because the denominator represents transpiration rather than stomatal conductance.	(13,53–55)
	Plant (Days to season; seasonal or)	 WUE _{plant}	Pot/Lysimeter	Ratio of net dry-matter production ($\approx$ NPP as biomass increment) to cumulative plant transpiration over the same period; i.e., “biomass produced per unit water transpired” at the whole-plant level	$WP_B/T = B/T$	Depends on biomass definition, plant developmental stage and experimental conditions. Not directly comparable with instantaneous leaf-scale metrics.	(39,56)
	Ecosystem (Sub-daily to daily;	 WUE _{eco-ET}	Eddy covariance	Ratio of Gross primary productivity (GPP) to evapotranspiration	GPP/ET	ET includes transpiration, soil evaporation and canopy interception; therefore it is not directly equivalent to GPP/T or leaf-scale WUE.	(37,46,57–64)
	Ecosystem (Sub-daily to daily;	 IWUE _{eco}	Eddy covariance + VPD adjustment	Ratio of Gross primary productivity (GPP) to evapotranspiration	$(GPP*VPD)/ET$	Retains the limitations of GPP/ET and depends on VPD normalization.	(5,6,18,20,36,65)
	Ecosystem (Sub-daily to daily; seasonal to	 δ WUE _{eco-ET}	Eddy covariance + linear VPD normalization	Ecosystem WUE normalized by $\sqrt{VPD}$, following the commonly used assumption of a fixed stomatal optimality exponent.	$(GPP*\sqrt{VPD})/ET$ or $GPP*VPD^{0.5}/ET$	The $\sqrt{VPD}$ relationship is based on an assumed stomatal response and may vary with environmental and hydraulic conditions.	(6,66,67)

Table 1 (continued)

Model-derived	Canopy / Ecosystem (Sub-daily to daily; seasonal to annual)		WUE_{gs}^{mod}	Process-based land-surface / ecosystem model	⁽¹⁾ Ratio of GPP and stomatal conductance at the canopy scale	GPP/g_s	Depends on model representation or estimation of GPP and canopy conductance.	(10,19,24,68–71)
	Canopy (Daily to seasonal or annual)		WUE_{can}^{mod}	Process-based land-surface / ecosystem model	Ratio of net primary production (NPP) to canopy transpiration	NPP/T	Depends on model representation of carbon allocation, NPP, canopy transpiration and canopy structure. NPP/T should not be treated as equivalent to GPP/T.	(24,72)
	Ecosystem (Daily to seasonal or annual)		WUE_{eco-T}^{mod}	Process-based land-surface / ecosystem model	Ratio of GPP to canopy transpiration	GPP/T	Directly depends on model representation of GPP, canopy conductance and transpiration. Comparability with empirical GPP/T requires consistent temporal aggregation and T definitions.	(5,24,63,72,73)
	Ecosystem (Daily to seasonal or annual)		WUE_{eco-ET}^{mod}	Process-based land-surface / ecosystem model	Ratio of GPP to canopy evapotranspiration	GPP/ET	Depends on model representation of GPP and all components of ET. Differences in ET partitioning can generate discrepancies with eddy-covariance WUE_{eco-ET} even when the same ratio is used.	(14,22,59,64,74)
Remote sensing	Ecosystem / regional to global		WUE_{modis}	Satellite-derived productivity and ET	WUE derived from satellite estimates of productivity and ET; formulation depends on the products used	NPP/ET GPP/ET	Depends on the algorithms and assumptions embedded in satellite products; GPP/ET and NPP/ET should not be treated as equivalent.	(75–79)
Optimality-based	Leaf → plant community				Stomatal optimality framework; estimated from sensitivities of E and A to g_s ; can be evaluated using gas exchange, isotopes or models	$\lambda = \partial E / \partial A = (\partial E / \partial g_s) / (\partial A / \partial g_s)$	Not a ratio-based WUE formulation. Provides a mechanistic perspective on water-use strategy, but depends on assumptions about stomatal regulation, photosynthesis and the relevant temporal/organizational scale	(1–4)

(1) WUE_{gs}^{mod} requires both GPP and canopy stomatal conductance. While eddy covariance provides latent heat flux (LE) as an observational constraint, GPP is typically derived from flux partitioning algorithms and g_s is obtained by inverting the Penman–Monteith equation. Neither variable is directly measured. This metric therefore occupies an intermediate position between empirical and modelled approaches and should be interpreted accordingly

climate change, as increasing atmospheric demand, altered soil moisture regimes, and changing plant physiological responses, can affect the carbon and water fluxes underlying different WUE formulations. A harmonized framework therefore needed to make these differences explicit and to support transparent comparisons across observational, experimental, and modeling approaches. In this review, we take steps toward this goal by synthesizing commonly used WUE definitions into a harmonized glossary (Table 1) and by providing a supplementary conversion guide that clarifies assumptions required to compare or translate among metrics (Table S1). Together, these resources provide a foundation for more transparent cross-disciplinary integration of WUE across scales.

Conceptual Framework and Definitions

The concept of the “water requirements of plants” first emerged in the agricultural literature in 1913 [36], when it was defined as the ratio of plant dry matter production to the amount of water used through transpiration. Since then, a wide array of definitions and formulations of WUE have emerged (see Table 1 for an overview). These multiple definitions include instantaneous leaf WUE (WUE_{leaf}), intrinsic WUE ($iWUE$), ecosystem-scale WUE (WUE_{eco}), and VPD-adjusted stomatal WUE ($iWUE_{VPD}$). Each definition differs in terms of its formula, units, underlying assumptions, and the spatial and temporal scales at which it is applied or simulated, ultimately leading to differences in what the metric actually

represents, reflecting also the widening scope over time, such as understanding plant responses to climate change and the regulation of water and carbon fluxes within the Earth system.

Importantly, from the very beginning, methods for estimating WUE spanned across multiple organizational, hierarchical and observational scales, from individual leaf-level gas exchange measurements to ecosystem-level assessments using eddy covariance, remote sensing, or modelled data. This apparent variability presented and still presents major challenges for cross-study comparison and synthesis, highlighting the urgent need for conceptual clarity and standardized definitions across disciplines and studies. A search on Google Scholar returned over 7,430,000 results (data accessed: 2026, September 10), and 322,521 results in Web Of Science (data accessed: 2026, September 10) for the term “Water Use Efficiency”, highlighting both the immense scientific interest in the topic and the fragmentation of its definitions and applications.

Table 1 summarizes a comprehensive set of fourteen different WUE metrics used in both empirical studies and modelling approaches in agricultural and forest science. These metrics encompass WUE formulations derived from leaf – and stomatal-level physiological observations, stable isotope measurements, ecosystem-scale flux measurements, remotely sensed products, process-based models, and optimality-based approaches. We explicitly distinguish among empirical measurements, modelled, satellite and optimality-based approaches, because these approaches differ fundamentally in how WUE is estimated, constrained, and interpreted, even when they share a common conceptual definition of WUE. These four approaches and their relationships across observational, modelling, remote-sensing, and theoretical frameworks are illustrated in Fig. 1.

Empirical measurements are derived from direct observations of physiological processes or carbon and water fluxes, including leaf-level gas exchange, stable isotope measurements, and eddy-covariance observations. Consequently, empirical WUE estimates are constrained by measurement accuracy, sampling design, instrumental limitations, and site-specific conditions. Depending on the measurement technique, they may represent instantaneous physiological responses or WUE integrated over seasonal, annual, or longer timescales.

In contrast, **modelled WUE estimates** are generated using process-based vegetation or ecosystem models that represent physiological and ecosystem processes through explicit or implicit process formulations. These models can simulate variables such as photosynthesis, transpiration, stomatal conductance, and carbon and water fluxes, from which WUE can subsequently be calculated. Modelled approaches enable WUE to be estimated continuously across spatial and temporal scales that are difficult to capture through direct

observations. However, their estimates depend on model structure, parameterization, and assumptions concerning plant physiology, environmental responses, canopy structure, and ecosystem functioning.

Satellite-derived WUE estimates are obtained from remotely sensed observations and associated algorithms or products, including products based on the Moderate Resolution Imaging Spectroradiometer (MODIS). These approaches provide spatially extensive estimates that can extend from regional to global scales and can support analyses over long periods. However, satellite-derived WUE is not a direct measurement of WUE; rather, it is inferred from remotely sensed variables and/or derived carbon- and water-related fluxes. Consequently, its uncertainty depends on the accuracy of the remotely sensed inputs, retrieval algorithms, and the assumptions used to relate remotely sensed signals to underlying physiological and ecosystem processes.

Optimality-based WUE approaches, in turn, derive WUE from theoretical frameworks that assume plants adjust their physiological processes to optimize carbon gain relative to water loss under environmental constraints. These approaches therefore differ from both direct observations and conventional process-based simulations because WUE emerges from an assumed optimization principle rather than being calculated solely from measured or prescribed fluxes. Their estimates depend on the formulation of the optimization objective, the environmental and physiological constraints imposed, and assumptions regarding plant adaptation, resource allocation, and the regulation of carbon and water exchange.

This methodological distinction is important because it directly affects uncertainty of characterization, scale of representativeness, and interpretability. Observations provide reality-based constraints but are often limited in spatial and temporal coverage, whereas modelled and satellite-derived approaches allow broader and more continuous assessments but depend on model formulations, retrieval algorithms, and underlying assumptions. Optimality-based approaches provide an additional theoretical perspective on WUE by linking observed or simulated patterns to hypothesized plant strategies. Separating these approaches therefore enables a clearer evaluation of agreement and divergence among WUE estimates and helps identify whether discrepancies arise from measurement limitations, remote-sensing retrievals, model structure and parameterization, or theoretical assumptions.

The distinction is therefore methodological rather than conceptual: the different approaches may quantify related aspects of the same underlying relationship between carbon gain and water loss, but they do so by using different sources of information and different assumptions. This distinction is essential for transparency, traceability, and rigorous cross-comparison of WUE metrics across studies and scales.

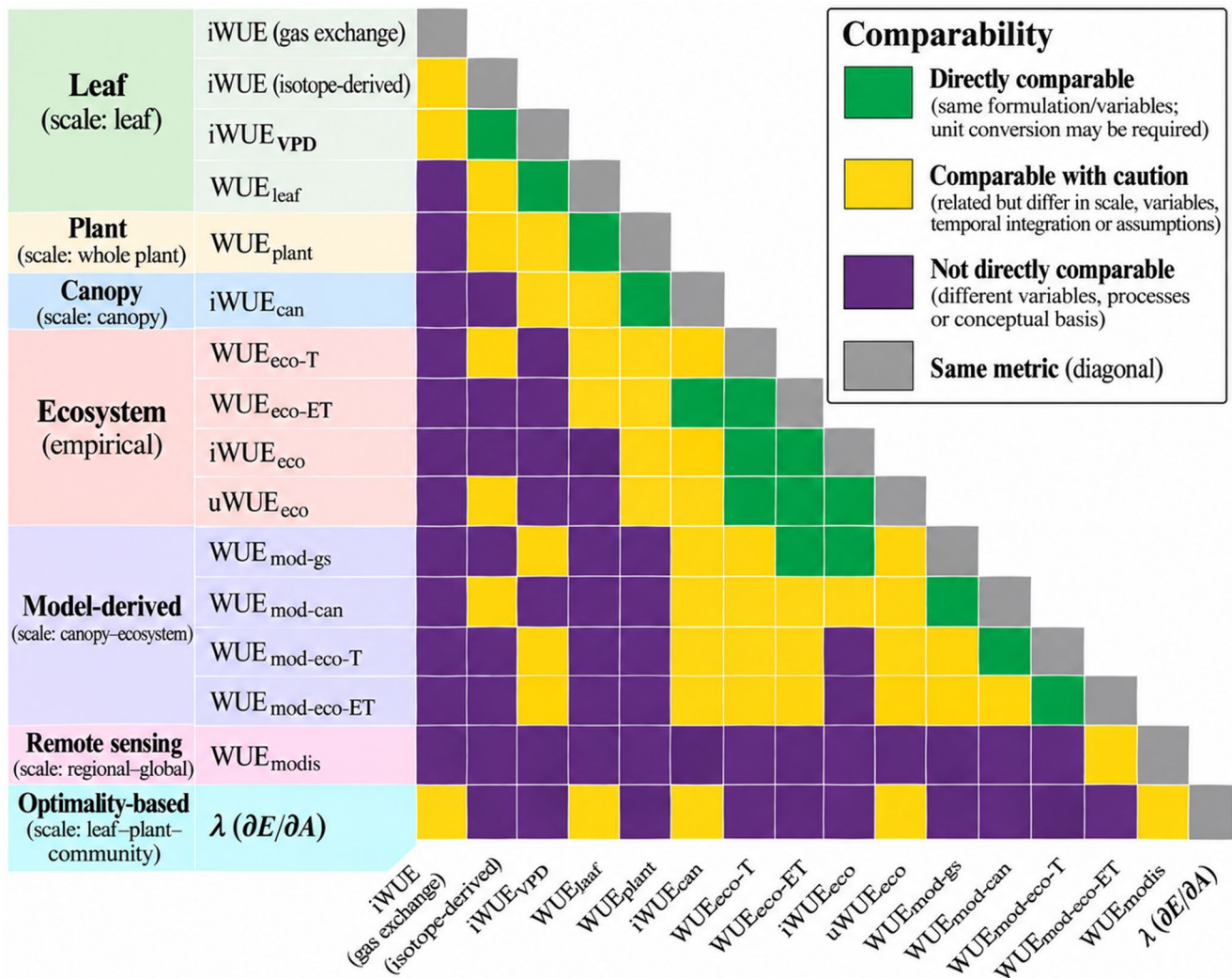


Fig. 1 Conceptual and operational comparability among WUE metrics. The triangular matrix illustrates the degree of comparability between pairs of WUE metrics. Green indicates direct comparability when metrics share the same formulation and variables, although unit conversion may be required; yellow indicates comparability with caution when metrics are conceptually related but differ in variables, spatial or temporal scale, temporal integration, normalization, or underlying assumptions; and purple indicates that metrics are not directly comparable because they quantify fundamentally different processes or quantities. Gray cells on the diagonal indicate the same metric. Metrics are

Overall, Table 1 highlights substantial differences among WUE metrics in their definitions, mathematical formulations, units, spatial scales, and temporal integration, all of which influence their interpretation and practical application. Empirical metrics generally provide direct, observation-based estimates at specific physiological or ecosystem scales; modelled metrics extend WUE estimation across scales through representations of underlying processes; satellite-derived metrics provide spatially extensive estimates based on remotely sensed information; and optimality-based metrics interpret WUE through theoretical assumptions about plant regulation

grouped according to their methodological and conceptual basis rather than their order in Table 1. The marginal water cost of carbon gain ($\lambda = \partial E / \partial A$) is included as a related optimality-based metric rather than as a ratio-based WUE formulation; its relationship with $iWUE$ reflects a shared focus on carbon–water trade-offs but does not imply numerical equivalence. Comparability categories are intended as a conceptual guide and may depend on the specific measurement conditions and assumptions. Detailed definitions, formulas, spatial and temporal scales, and key assumptions are provided in Table 1, while guidance for metric selection is given in the Recommendations section

and resource optimization. These methodological differences should therefore be considered when comparing WUE values across studies, as numerical similarities do not necessarily imply equivalence in the processes, scales, or assumptions represented by the respective metrics.

Key Differences and Discrepancies Across Time Scales

Several challenges complicate the comparison and interpretation of WUE metrics:

Temporal Integration Instantaneous WUE captures short-term gas exchange dynamics, whereas ecosystem WUE or tree-ring derived $\dot{\gamma}$ WUE, for example, integrate over longer periods (e.g., seasonal to annual), potentially masking important diurnal and seasonal variations [72]. These discrepancies complicate the interpretation, comparison and detection of climate feedback mechanisms and long-term trends.

Measurement Approaches Physiological measurements (e.g., leaf gas exchange) are direct and short-term, quantifying fluxes tied to transpiration or its controls (T , g_s). By contrast, model-derived metrics and remote sensing (e.g., Earth System Models [17] or MODIS products [74] integrate over broader spatial-temporal domains and rely on additional assumptions. Eddy covariance systems measure the total latent heat flux (LE), corresponding to evapotranspiration ($ET = E + T + \text{interception}$), whereas transpiration (T) alone is not directly accessible and must be estimated through partitioning approaches, including stable isotope techniques based on $\delta^{18}\text{O}$ or $\delta^2\text{H}$ of water vapor, sap flow measurements, or model-based algorithms. Uncertainty associated with T/ET partitioning propagates directly into $WUE_{\text{eco-T}}$ estimates and should therefore be explicitly reported. Where T partitioning is unavailable, $WUE_{\text{eco-ET}}$ (GPP/ET) remains the appropriate empirical metric, although it may differ systematically from transpiration-based WUE, particularly in ecosystems with high soil evaporation or canopy interception.

Inconsistencies Between Units and Variables Beyond simple unit conversions (e.g., $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ vs. $\text{gC kg}^{-1} \text{ H}_2\text{O}$), a larger source of divergence is which variables are used and how they are aggregated. Common mismatches include ET vs. T in the denominator; $g_s w$ (to H_2O) vs. $g_s c$ (to CO_2); A (leaf assimilation) GPP/NPP (gross and net productivity); instantaneous rates vs. seasonal/annual sums; leaf-area vs. ground-area normalization; VPD units (Pa vs. kPa, and exponents in WUE); and carbon vs. dry-mass bases. An additional source of inconsistency arises from assuming a fixed VPD exponent in ecosystem-scale WUE formulations such as underlying WUE_{u} (WUE). The commonly used normalization by $\sqrt{\text{VPD}}$ assumes a constant optimality exponent ($k=0.5$), derived from classical stomatal optimization theory. However, recent work [66] demonstrates that this exponent is highly dynamic and strongly influenced by soil water content, atmospheric drought, and species-specific hydraulic strategies. This suggests that fixed VPD corrections may oversimplify ecosystem carbon–water coupling, particularly in water-limited ecosystems.

A note on conductance basis: stomatal conductance is most commonly reported on a water vapor basis ($g_s w$, $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), as this is the default output of leaf gas exchange systems and directly reflects the water loss pathway. Some

formulations, particularly those derived from isotope-based or optimal stomatal theory, express conductance on a CO_2 basis ($g_s c = g_s w/1.6$), reflecting the lower diffusivity of CO_2 relative to H_2O in air. In this manuscript, we adopt $g_s w$ as the primary variable for all WUE formulations, consistent with the water-based definition of WUE. Where $g_s c$ appears in source literature, we convert explicitly using $g_s c = g_s w/1.6$ and note this conversion. Users should verify the conductance basis when comparing WUE values across studies, as mixing $g_s w$ and $g_s c$ without conversion introduces a systematic factor of 1.6 error in $\dot{\gamma}$ WUE estimates.

Mixing these choices yields non-comparable “WUE” values and can even invert trends across scales. Here we standardize by: (i) stating T vs. ET explicitly (preferring T for physiological inference), (ii) converting stomatal conductances to a CO_2 basis ($\div 1.6$ when needed), (iii) aligning rates to sums over the same period before forming ratios, and (iv) reporting a consistent unit set (gC m^{-2} for carbon; $\text{mm} \equiv \text{kg H}_2\text{O m}^{-2}$ for water). These conversions and their assumptions are detailed in Table S1.

Scaling Issues Transitioning from stomatal-level to ecosystem-level WUE is challenging because canopy structure, soil and interception evaporation, environmental heterogeneity, and land-atmosphere coupling alter the relationship between carbon gain and water loss. Several studies report substantial discrepancies between long-term $\dot{\gamma}$ WUE and WUE_{eco} [10, 15, 18, 43] indicating that processes measured at the stomatal/leaf/plant level and those inferred from ecosystem fluxes are not directly comparable [4, 16]. The use of ET rather than T in the denominator of ecosystem WUE has two distinct and sometimes opposing effects that must be carefully distinguished. First, because $ET > T$ (ET includes soil evaporation and canopy interception in addition to transpiration), substituting ET for T inflates the denominator and therefore tends to underestimate the absolute magnitude of WUE relative to transpiration-based formulations. Second, and separately, ecosystem-scale WUE metrics have been shown to overestimate the sensitivity of WUE to rising atmospheric CO_2 relative to stomatal-scale $\dot{\gamma}$ WUE [17, 18, 25, 78]. This occurs because CO_2 -driven stomatal closure reduces T proportionally more than it affects the non-transpirational components of ET , causing $WUE_{\text{eco-ET}}$ to respond more strongly to CO_2 than physiologically justified. These two effects, magnitude underestimation and sensitivity overestimation, operate in opposite directions and should not be conflated. Careful partitioning of ET into its components is therefore essential for accurate interpretation of ecosystem WUE trends.

In fact, recent studies show that increases in $\dot{\gamma}$ WUE do not necessarily translate into higher GPP or NPP, as the relationship between $\dot{\gamma}$ WUE and productivity depends strongly on

hydroclimatic constraints such as VPD and plant hydraulic limitations [70]. This highlights that scaling WUE across organizational levels is inherently complex and prone to divergent interpretations when definitions and drivers are not explicitly harmonized. This is particularly relevant for μ WUE approaches, where the assumption of a constant VPD correction may not hold across scales or drought intensities, leading to systematic over- or underestimation of ecosystem WUE [66]. Consequently, caution is required when interpreting physiological metrics across scales, and models must explicitly represent T versus ET partitioning, canopy conductance, and carbon-allocation processes.

Recommendations

To enhance consistency, comparability, and scientific value in WUE research, the following recommendations are proposed:

Standardization of Reporting When reporting WUE, authors should adhere to the following minimum standards.

- State the exact formula used, including whether the denominator is g_w , g_c , T, or ET;
- Specify the temporal scale (instantaneous, daily, seasonal, annual) and spatial scale (leaf, plant, canopy, ecosystem);
- Report the units explicitly and verify consistency with the formula (e.g., avoid mixing molar and mass-based units without conversion);
- Indicate whether VPD normalization has been applied and justify the choice of VPD exponent;
- For ecosystem metrics, report the T/ET ratio of the study site where available, as this directly affects comparability with leaf- or plant-scale WUE.

Developing a community-wide consensus on WUE definitions, variables, units, and reporting standards is essential to enhance comparability across studies and ensure relevance for climate modeling, Earth system science, and eco-physiological applications. Here, we provide a first step by proposing unique variable names, abbreviations, harmonized definitions, and formulas to which refer (Table 1), together with a supplementary conversion guide that clarifies assumptions and enables transparent translation across metrics (Table S1). Promoting the use of standardized abbreviations and formulas across disciplines will reduce conceptual fragmentation and facilitate cross-scale integration, ultimately improving the robustness of WUE-based analyses.

Metric Selection Guidance The choice of WUE metric should always be guided by the specific research question, the available data, and the spatial and temporal scale of the

study. No single WUE formulation is universally superior; rather, each metric captures a distinct aspect of carbon–water coupling and is most informative within its intended context.

At the leaf and stomatal scale, where the primary interest lies in physiological responses to environmental drivers such as CO_2 , temperature, or drought, intrinsic WUE defined as $iWUE = A/g_w$ is the most appropriate metric. It can be derived from direct leaf gas exchange measurements or from carbon isotope discrimination in plant tissues, including tree-ring cellulose, making it particularly valuable for long-term retrospective analyses.

At the whole-plant or crop scale, where the focus is on biomass production relative to water consumed, $WUE_{plant} = B/T$ derived from lysimeter or pot experiments provides the most direct and interpretable measure of water productivity.

At the ecosystem scale, the choice between transpiration-based and evapotranspiration-based formulations is critical and should be made explicitly. When transpiration can be independently estimated through partitioning approaches such as sap flow measurements, isotopic methods, or model-based algorithms, $WUE_{eco-T} = GPP/T$ is preferred because it most closely reflects the physiological process of stomatal carbon–water exchange and avoids the confounding influence of soil evaporation and canopy interception. When only total evapotranspiration is available, as is typically the case with eddy covariance measurements, $WUE_{eco-ET} = GPP/ET$ remains the appropriate empirical metric, provided that users explicitly acknowledge that $ET > T$ and that absolute WUE values derived from this formulation are not directly comparable to transpiration-based metrics without applying the f_T correction described in Table S1.

Finally, for studies aimed at comparing WUE across contrasting climatic gradients or at removing the confounding effect of atmospheric evaporative demand, VPD-normalized formulations such as $IWUE_{eco} = GPP \times VPD/ET$ or $\mu WUE_{eco} = GPP \times \sqrt{VPD/ET}$ are recommended. However, users should carefully evaluate whether the fixed VPD exponent assumption ($k=0.5$) is appropriate for their ecosystem type, particularly in water-limited systems where this exponent has been shown to vary dynamically with soil moisture and hydraulic stress [66].

Cross-Scale Integration Encourage studies that bridge spatial and temporal scales by co-locating measurements and validating model outputs with independent data from field physiology (leaf gas exchange, sap-flow/lysimeter T), eddy-covariance (ET/LE), remote sensing measurements, and long-term networks. At minimum, provide a process-based map of how metrics relate—the carbon pathway ($A \rightarrow GPP \rightarrow NPP \rightarrow \Delta B$), the water pathway ($ET = E +$

T+interception vs. T), the conductance basis ($g_{sw} \leftrightarrow g_{sc}$ via 1.6), temporal aggregation (rates vs. sums), area basis (leaf vs. ground), and any VPD normalizations. Providing functional relationships and process-based information on similarities and differences between these metrics is essential for enabling transparent and robust conversions by specialists (Table S1).

Concluding Remarks and Future Perspectives

WUE has become a widely used metric for understanding vegetation functioning under global change. Beyond its ecological relevance, the broader concept of water-use efficiency is also explicitly embedded in international policy frameworks, including UN Sustainable Development Goal Target 6.4 and Indicator 6.4.1 [80], for which FAO is the custodian agency, reflecting its relevance to sustainable water management, food security, ecosystem functioning, and climate resilience [81]. This is particularly critical under climate change, where increasing atmospheric CO₂ concentration, rising temperatures, and more frequent and severe drought events alter plant water-carbon dynamics across all ecosystems. These changes further amplify the need for robust and comparable WUE metrics to support reliable projections and adaptation strategies. In this review, we highlighted the diversity of WUE formulations and demonstrated that differences in variables, spatial and temporal scales, measurement approaches, and underlying assumptions can lead to substantially different interpretations of apparently similar WUE metrics. We therefore emphasize the need for a harmonized, terminology, and transparent methodological framework that preserves the specific conceptual meaning of each metric rather than treating WUE as a single, universally interchangeable quantity. We contribute to this goal by providing a standardized glossary of unique variable names, abbreviations, and definitions, and formulas (Table 1), together with a supplementary conversion guide (Table S1) that clarifies assumptions and enables transparent translation and comparison among metrics where such conversions are scientifically justified.

Moving forward, a key priority is the co-development of a unified WUE framework that acknowledges scale-specific contexts while promoting interoperability across empirical modelled estimates, satellite-derived products, and optimality-based approaches. Such a framework should explicitly account for the process represented by the metric, including the distinction between transpiration (T) and evapotranspiration (ET), the basis of stomatal conductance (g_{sw} versus g_{sc}), temporal aggregation, spatial normalization, and VPD normalization. The next steps are to better

understand the process-based relationships and differences between WUE metrics, and to develop community guidelines that standardize not only reporting practices but also the conditions and assumptions under which conversions across definitions are appropriate (as outlined in Supporting Table S1). Expanding the use of isotopic tracers, remote sensing, coordinated field observations, and process-based modelling will also be crucial to reconcile observations with simulations and to improve scaling from leaf to ecosystem and global levels. Importantly, integration across these approaches should focus not only on numerical agreement among WUE estimates, but also on whether they represent comparable carbon and water processes, scales, and temporal integrations.

Our synthesis further shows that cross-scale comparisons require caution. Metrics derived at the leaf or stomatal scale cannot necessarily be interpreted as direct proxies for ecosystem-scale WUE, because canopy structure, soil evaporation, interception, atmospheric demand, hydraulic constraints, and carbon allocation can alter the relationship between carbon gain and water loss. Similarly, satellite-derived and modelled estimates provide valuable spatial and temporal coverage but incorporate retrieval algorithms, parameterizations, and structural assumptions that should be explicitly recognized when comparing them with empirical measurements. Optimality-based formulations provide a complementary theoretical perspective, but their interpretation depends on the optimization principles and constraints adopted. Thus, differences among WUE estimates should not automatically be interpreted as inconsistencies; they may instead reflect differences in the processes, scales, or assumptions represented by each metric.

It should also be emphasized that there is no inherent hierarchy of “pros and cons” among different WUE formulations, as their interpretation strongly depends on the specific conceptual and methodological framework underpinning each approach, rather than on simple performance comparisons or prescriptive recommendations.

Collaborative, interdisciplinary efforts, even between science and policy, will be essential to advance consistent interpretation of WUE across spatial and temporal scales. By integrating standardized definitions (Table 1), transparent conversion rules (Table S1), and future guidelines for cross-metric translation, we aim to strengthen scientific communication, improve the interpretation of vegetation carbon–water interactions across spatial and temporal scales. Ultimately, a more coherent WUE framework should not seek to eliminate methodological diversity, but rather to make that diversity explicit, traceable, and scientifically interpretable, enabling more robust integration of observations, models, remote sensing, and theoretical approaches.

Glossary

WUE definitions

WUE	Generic water use efficiency [various units depending on scale and formulation].
i WUE	Stomatal scale intrinsic water use efficiency [$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$] or [$\mu\text{mol mol}^{-1}$].
i WUE _{VPD}	Stomatal scale intrinsic water use efficiency, adjusted by VPD [$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$].
WUE _{leaf}	Instantaneous leaf scale water use efficiency [$\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$] or [$\text{g C kg}^{-1} \text{ H}_2\text{O}$].
WUE _{plant}	Whole-plant water use efficiency [$\text{g DM m}^{-2} \text{ mm}^{-1}$] or [kg DM m^{-3}].
i WUE _{can}	Canopy-scale water use efficiency computed using stomatal conductance [$\text{g C kg}^{-1} \text{ H}_2\text{O}$]. If GPP in g C and g_s , can expressed as water flux equivalent) or [$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ (molar basis)].
WUE _{eco}	Ecosystem scale water use efficiency [various units depending on formulation].
WUE _{eco-T}	Ecosystem scale water use efficiency computed using transpiration [$\text{g C kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
WUE _{eco-ET}	Ecosystem scale water use efficiency computed using evapotranspiration [$\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$] or [$\text{g C kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
IWUE _{eco}	Ecosystem Inherent water use efficiency [$\text{g C kPa m}^{-2} \text{ mm}^{-1}$] or [$\text{g C kg}^{-1} \text{ H}_2\text{O kPa}^{-1}$].
u WUE _{eco}	Ecosystem underlying water use efficiency with linear VPD normalization [$\text{g C mm}^{-1} \text{ H}_2\text{O kPa}^{0.5}$].
WUE _{gs} ^{mod}	Simulated Ecosystem scale water use efficiency computed using canopy stomatal conductance [$\text{g C Kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
WUE _{can} ^{mod}	Simulated canopy scale water use efficiency computed as the ratio of NPP / T [$\text{g C Kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
WUE _{eco-T} ^{mod}	Simulated ecosystem scale water use efficiency computed as the ratio of GPP / T [$\text{g C Kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
WUE _{eco-ET} ^{mod}	Simulated ecosystem scale water use efficiency computed as the ratio of GPP / ET [$\text{g C Kg}^{-1} \text{ H}_2\text{O}$] or [$\text{g C mm}^{-1} \text{ H}_2\text{O}$].
WUE ^{modis}	Satellite-derived ecosystem-scale water use efficiency using MODIS NPP and T products [$\text{mg C m}^{-2} \text{ mm}^{-1}$].

Variables

A	Net carbon assimilation [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$].
g_{sw}	Stomatal conductance to water vapor [$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$] or [$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$]. Default output in leaf gas-exchange systems.
g_{sc}	Stomatal conductance to CO_2 [$\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$] or [$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$]. For the stomatal pathway, g_{sc} is conventionally calculated as $g_{sw}/1.6$ to account for the different diffusivities of H_2O and CO_2 in air. This relationship applies to the stomatal pathway and should not be interpreted as a general conversion between total leaf H_2O and CO_2 conductance when cuticular conductance is present.
g_{cw}	Cuticular conductance to water vapour [$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$] or [$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$]. Represents water-vapour transport through the leaf cuticle independently of the stomatal pathway.
T	Leaf or Canopy transpiration [$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$] or [mm h^{-1}] or [mm day^{-1}] or [mm yr^{-1}]. Short-term fluxes in molar units; integrated periods in mm.
ET	Evapotranspiration [mm day^{-1}] or [mm yr^{-1}].
GPP	Gross primary production [$\text{g C m}^{-2} \text{ yr}^{-1}$].
NPP	Net primary production [$\text{g C m}^{-2} \text{ yr}^{-1}$].
VPD	Vapor pressure deficit [Pa] or [kPa]. kPa is commonly used; Pa is physically correct but less intuitive.
C_a	Ambient CO_2 concentrations [$\mu\text{mol mol}^{-1}$] or [Pa].
C_i	Intercellular CO_2 concentrations [$\mu\text{mol mol}^{-1}$] or [Pa].
LE	Latent heat flux W m^{-2} (instantaneous flux) or MJ m^{-2} over an integrated period (e.g., daily or seasonal)
WPB/Tr	Water productivity as the ratio of biomass to transpiration [$\text{g DM m}^{-2} \text{ mm}^{-1}$] or [kg DM m^{-3}]
B	Total crop biomass [$\text{gDM m}^{-2} \text{ day}^{-1}$].
λ	(marginal water cost of carbon gain) Marginal water cost of carbon gain, defined as the additional water loss associated with an incremental unit of carbon gain: $\lambda = \partial A / \partial E = \partial A / \partial g_s \partial E / \partial g_s$ [$\text{mol H}_2\text{O mol}^{-1} \text{ CO}_2$ or equivalent units]. Unlike

ratio-based WUE metrics, λ characterizes water-use strategy from the marginal relationship between carbon assimilation and water loss [26, 79, 27, 5]

Unit convention Throughout the manuscript we report carbon fluxes on a ground-area basis as $\text{g C m}^{-2} \text{ time}^{-1}$ and water fluxes as mm time^{-1} (with $1 \text{ mm} \equiv 1 \text{ kg H}_2\text{O m}^{-2}$). Where conductances are used, we report $g_s w$ in $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and convert to a CO_2 basis as $g_s c = g_s w / 1.6$

Nomenclature logic for prefixes and suffixes

- Prefix λ (lowercase) reserved exclusively for intrinsic metrics, i.e., those normalized by stomatal conductance ($g_s w$ or $g_s c$) rather than by a water flux. Example: $\lambda WUE = A_n / g_s w$.
- Prefix I (uppercase) reserved for Inherent ecosystem WUE, specifically the formulation $IWUE_{eco} = GPP \cdot VPD / ET$, following Beer et al. [62].
- Prefix u reserved for underlying ecosystem WUE, specifically $uWUE_{eco} = GPP \cdot \sqrt{VPD} / ET$, following Zhou et al. [63].
- Suffix $_{eco}$ denotes ecosystem scale, typically derived from eddy covariance or remote sensing.
- Suffix $_{can}$ denotes canopy scale, typically derived from canopy conductance or canopy-level flux estimates.
- Suffix $_{mod}$ denotes model-derived (simulated) metrics.
- Suffix $_{modis}$ denotes metrics derived specifically from MODIS satellite products.
- Subscripts -T and -ET explicitly indicate whether transpiration (T) or evapotranspiration (ET) is used in the denominator. This distinction is mandatory and should always be reported.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40641-026-00210-z>.

Acknowledgements PFP received three grants through work conducted within the COST ACTION CA21138 (CLEANFOREST) “Joint effects of CLimate Extremes and Atmospheric deposition N on

European FORESTS”, supported by COST (European Cooperation in Science and Technology). PFP and AC were supported by the MIUR project (PRIN 2020) “Unraveling interactions between WATER and carbon cycles during drought and their impact on water resources and forest and grassland ecosystems in the Mediterranean climate” (WATERSTEM, Grant No. 20202WF53Z) and the (PRIN 2022) project “Unravelling seasonal to decadal CLimate influence on the Carbon cycle in FOrEst. A multidisciplinary analysis across contrasting climates” (ClicFor, Grant No. 2022ETAB7T).

Author Contributions P.F.P. Conceptualization, Visualization, Writing – Original Draft; M.S. Writing – Review & Editing; A.C. Conceptualization, Project management and Writing – Review & Editing. All authors contributed to reviewing the text and figures.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Human and Animal Rights This article does not contain any studies with human or animal subjects performed by any of the authors.

Declaration of Generative AI and AI-assisted Technologies in the Writing Process During the preparation of this work, the authors used ChatGPT (OpenAI) to improve the readability and clarity of the manuscript. After using this tool, the authors carefully reviewed and edited the content as needed and took full responsibility for the content of the published article.

Competing interests The authors declare no competing interests.

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