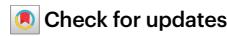


# Rethinking microbial carbon use efficiency in soil models

Steven D. Allison



Soil models include a key parameter known as carbon use efficiency, which impacts estimates of global carbon storage by determining the flow of carbon into soil pools versus the atmosphere. Microbial-explicit versions of these models are due for an update that recasts carbon use efficiency as an output variable emerging from microbial metabolism.

In ecosystem models, the partitioning of carbon into soil pools versus carbon dioxide is governed by a key parameter known as carbon use efficiency (CUE; Box 1). When carbon moves from one pool to another – for example, from dead plants into soil organic matter – CUE represents the fraction of carbon transferred. If CUE is 0.1, then 10% of

the carbon enters the soil pool and 90% flows into the atmosphere as carbon dioxide.

Until 2010, ecosystem models assumed that CUE was a constant parameter<sup>1</sup>. Over the past 15 years, that assumption has proved to be false for two main reasons. First, CUE is now known to be an emergent property of the diverse microbial communities residing in soil<sup>2</sup>. Second, microbial communities are sensitive to temperature, moisture, substrate chemistry and other environmental variables, meaning that emergent CUE can vary as climate changes. Considering these conceptual advances, the next generation of soil models should reframe CUE as a predicted variable rather than a simplified proxy for microbial physiology.

## CUE and the carbon–climate feedback

With soils storing around 2,000 Pg of organic carbon globally, altering the efficiency of soil carbon cycling by microorganisms could have implications for climate change<sup>1</sup>. Soil microorganisms play two

## BOX 1

### Defining CUE

A recent study<sup>6</sup> defines CUE in terms of time (*t*)-dependent carbon (C) balance of an organism, community or ecosystem compartment:

$$\frac{dC}{dt} = U - EG - R - EX - T \quad (1)$$

with rates *U* = carbon uptake, *EG* = egestion (that is, excreted waste), *R* = respiration, *EX* = exudation (secretion of biomolecules) and *T* = turnover (that is, cellular death or predation). The net biomass growth rate *G* is defined as:

$$G = U - EG - R - EX \quad (2)$$

Because we are not focusing on animals, let us assume *EG* = 0 for simplicity. The CUE of soil microorganisms is then:

$$\text{CUE} = (U - R - EX)/U = G/U \quad (3)$$

Note that some definitions<sup>6</sup> include *EX* in the computation of CUE, but *EX* is subtracted here because it does not contribute directly to *G*. The *R* term can be broken down further into different sources of respiration from uptake machinery (*R<sub>U</sub>*), biomass maintenance (*R<sub>B</sub>*) and enzyme + protein synthesis (*R<sub>E</sub>*)<sup>8</sup>:

$$\text{CUE} = (U - R_U - R_B - R_E - EX)/U \quad (4)$$

In some models, *R<sub>B</sub>*, *R<sub>E</sub>* and *EX* are assumed to be negligible or part of *R<sub>U</sub>*, leading to a term defined here as carbon assimilation efficiency, *CUE<sub>A</sub>*:

$$\text{CUE}_A = (U - R_U)/U \quad (5)$$

The mass balance principles underlying CUE also apply at ecosystem scales. For instance, first-order soil carbon models use a CUE parameter equivalent to:

$$\text{CUE} = (I - R)/I \quad (6)$$

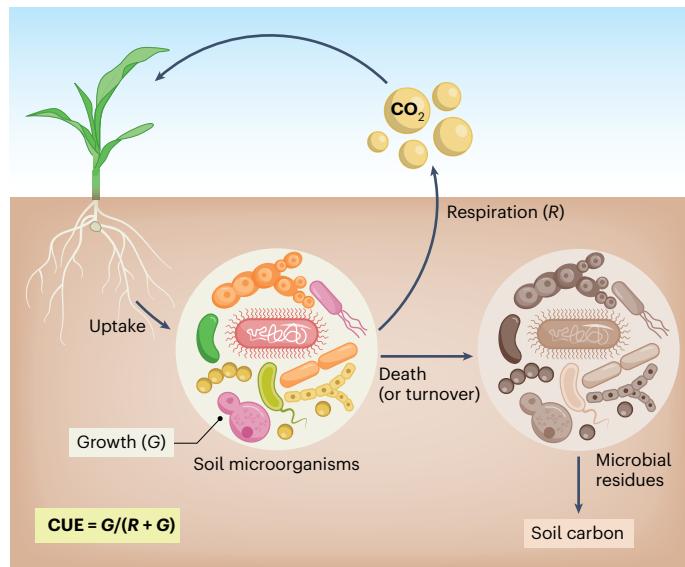
where *I* represents the carbon input rate to a soil compartment, analogous to *U* in equation (5). Ecosystem CUE (*CUE<sub>Ecosystem</sub>*) can be defined as net ecosystem production (NEP) divided by gross primary production (GPP):

$$\text{CUE}_{\text{Ecosystem}} = \text{NEP}/\text{GPP} \quad (7)$$

where NEP is analogous to *G* and GPP is analogous to *U* in equation (3). Similarly, plant CUE (*CUE<sub>Plant</sub>*) can be defined as:

$$\text{CUE}_{\text{Plant}} = \text{NPP}/\text{GPP} \quad (8)$$

where NPP is net primary production, again analogous to *G/U*.



**Fig. 1 | Partitioning of soil carbon into microbial biomass versus carbon dioxide (CO<sub>2</sub>).** Soil microorganisms take up carbon from soil and plants, converting it into biomass during growth (G) and respiring CO<sub>2</sub> through metabolism (R), processes that are sensitive to climate and soil conditions. Dead microorganisms form residues that contribute to soil carbon accrual.

opposing roles in the carbon cycle (Fig. 1). For one, they convert organic matter into carbon dioxide (and sometimes methane), often with the help of extracellular enzymes that break down complex polymers. But soil microorganisms also build biomass when they grow. If their biomass is more resistant to decay than the carbon they consume, microorganisms can help boost soil carbon storage.

These dual roles raise an important question about CUE: are more efficient microorganisms good or bad for soil carbon storage? Higher CUE means microorganisms can build more biomass, which might enter long-lived soil carbon pools. However, raising the CUE of microbial decomposers could lead to faster rates of soil carbon turnover and more greenhouse gas emissions.

Current models do not agree on which outcome dominates. Traditional models of the soil carbon cycle, such as Century, only represent the carbon accrual mechanism. In those models, higher CUE always leads to greater soil carbon storage because decay rates do not depend on microbial biomass. Newer 'microbial explicit' soil models assume that decay rates depend on microbial biomass, meaning that soil carbon stocks may increase, stay constant or even decline as CUE increases<sup>3</sup>. Observations are not definitive either. A recent global data synthesis<sup>4</sup> found a positive correlation between soil carbon stocks and microbial CUE, but the causal mechanism underlying that relationship has been questioned<sup>5</sup>.

## Modelling CUE

Even as the soil carbon–CUE relationship remains controversial, soil models have been updated to better represent key microbial processes<sup>1</sup>. Compared with traditional first-order models, microbial-explicit models of the soil carbon cycle are more consistent with fundamental knowledge and empirical data<sup>3</sup>. They also predict different carbon responses to perturbations such as warming and increased plant inputs, highlighting the importance of accurately modelling microbial processes.

Still, the parameterization of microbial physiology remains rudimentary even in these updated models. Apart from a simple (and uncertain) linear dependence on temperature, CUE in the latest models has hardly advanced beyond previous single parameter assumptions. Consequently, there is still a wide gap between current biological understanding of microorganisms and their parameterization in models. This gap is problematic because the modelled predictions of carbon dynamics, and potentially real soil carbon stocks, are highly sensitive to microbial parameters such as CUE.

To improve predictions, the next generation of soil models should represent CUE as an emergent property of underlying processes at different scales<sup>2,6,7</sup>, not a single parameter or simple linear function. Like traditional models, microbial-explicit models have used CUE as a convenient proxy for the complex cellular physiology of bacteria and fungi. A more realistic model structure would break up CUE into component parts that correspond to measurable pathways of microbial carbon uptake and loss. That way, the well-studied physiological responses of microorganisms to environmental change could be represented with high fidelity, ensuring that updated models make the right predictions for the right reasons.

Such an approach reframes CUE as a model output rather than an input. Physiological studies show that CUE – and other microbial properties crucial for soil carbon storage – emerges from metabolic pathways governing protein synthesis, nucleic acid synthesis, stress response and substrate metabolism, to name a few<sup>8</sup>. For instance, drought-induced desiccation reduces cellular carbon uptake, while physiological mechanisms of drought tolerance elevate energetic costs that reduce CUE<sup>9</sup>. Additionally, thermal stress can affect CUE, although there is considerable debate in the literature about the magnitude and direction of the temperature–CUE relationship<sup>10</sup>. Substrate stoichiometry also matters, with wider carbon:nutrient ratios often reducing CUE. Reframing CUE as an output would open the door to validating mechanistic microbial models with empirical observations of CUE response to these changes in climate and substrate chemistry.

## Research priorities for CUE

Replacing the proxy parameter version of CUE with realistic microbial metabolism will not be trivial. To make progress, future research should prioritize multiscale modelling combined with targeted empirical measurements. This work can leverage the recent explosion of microbial genomic sequencing data and the proliferation of genome-enabled metabolic models<sup>11</sup>.

Genomic data can be harnessed to build models of microbial metabolism – including emergent CUE – and its response to global change drivers<sup>12</sup>. Whole genome sequences derived from microbial isolates or metagenome-assembled genomes are now available for tens of thousands of bacteria and fungi, with the numbers growing every day. These sequences provide the basis for genome-scale metabolic models that estimate substrate use and respiration rates, enabling data-driven predictions of emergent CUE at the population level.

With genome-derived predictions in hand, the next key step is scaling up these population parameters to the community level. Although genome-scale metabolic models are not designed to make soil carbon predictions, trait-based microbiome models are well suited for this task. Such models represent soil spatial structure along with changes in temperature, moisture and substrates that affect the physiological rates underlying CUE and other emergent properties relevant for carbon cycling by soil microbiomes<sup>9</sup>.

Microbiome models – along with observational data – show that shifts in microbial community composition will impact soil carbon responses to global change<sup>9,13</sup>. As climate and other variables change with time or along spatial gradients, microorganisms with distinct physiological traits are favoured, potentially driving changes in emergent CUE at the community scale. In addition to community changes, evolutionary processes may be important. For instance, microbial populations can evolve in response to changing climate or other environmental conditions<sup>14</sup>. If there is evolutionary selection on CUE – that is, if more efficient microorganisms have higher fitness in a particular environment – then models of emergent CUE and soil carbon cycling will need to consider evolutionary change on decadal to century timescales.

Finally, microbial community models must be scaled up to predict changes in the global carbon cycle. The scaling approach should account for global environmental gradients with special attention to wetland, permafrost and deep tropical soils that store most of the world's organic carbon<sup>15</sup>. So far, computational and conceptual limitations have precluded the representation of time-varying, emergent biological properties in Earth system models. However, climate scientists are tackling analogous problems within the physical components of the Earth system, such as parameterization of sub-grid-scale ocean eddies and cloud feedbacks. Computational advances in model emulation, artificial intelligence and processor speed should make it possible to couple more realistic microbial-scale models with land surface models running at ecosystem to Earth system scales.

## Conclusion

To align better with current knowledge, soil carbon models should represent CUE as an emergent property of multiple interacting biological and physical processes. By reframing CUE as an output variable instead of an input parameter, the next generation of microbial-explicit models can focus on the key, measurable physiological processes that matter

for soil carbon cycling. Rapid advances in genomics will be helpful in building these updated models, although there are still challenges with model complexity and scaling. Model designers must determine which microbial pathways are most critical for predicting emergent CUE, or other key traits, and how to represent them at broad scales. Although these are daunting challenges, addressing them will help to ensure that new models reflect current knowledge, leading to better soil carbon predictions at the global scale.

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## Competing interests

The author serves on the Scientific Advisory Board for Ginkgo Bioworks, Inc.