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Microbial carbon use efficiency: accounting for population, community, and ecosystem-scale controls over the fate of metabolized organic matter

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Abstract Microbial carbon use efficiency (CUE) is a critical regulator of soil organic matter dynamics and terrestrial carbon fluxes, with strong implications for soil biogeochemistry models. While ecologists increasingly appreciate the importance of CUE, its core concepts remain ambiguous: terminology is inconsistent and confusing, methods capture variable temporal and spatial scales, and the significance of many fundamental drivers remains inconclusive. Here we outline the processes underlying microbial efficiency and propose a conceptual framework that structures the definition of CUE according to increasingly broad temporal and spatial drivers where (1) CUE_P reflects population-scale carbon use efficiency of microbes governed by species-specific metabolic and thermodynamic constraints, (2) CUE_C defines community-scale microbial efficiency as gross

biomass production per unit substrate taken up over short time scales, largely excluding recycling of microbial necromass and exudates, and (3) CUE_E reflects the ecosystem-scale efficiency of net microbial biomass production (growth) per unit substrate taken up as iterative breakdown and recycling of microbial products occurs. CUE_E integrates all internal and extracellular constraints on CUE and hence embodies an ecosystem perspective that fully captures all drivers of microbial biomass synthesis and decay. These three definitions are distinct yet complementary, capturing the capacity for carbon storage in microbial biomass across different ecological scales. By unifying the existing concepts and terminology underlying microbial efficiency, our framework enhances data interpretation and theoretical advances.

Keywords Carbon use efficiency · Microbial metabolism · Carbon cycling · Microbial ecology

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Introduction

The efficiency with which microorganisms convert available organic substrates into stable, biosynthesized products (broadly defined as ‘carbon use efficiency’—CUE) is a critical step in ecosystem carbon cycling. Microbes metabolize a wide variety of compounds to satisfy heterotrophic demands for carbon (C) and energy, thereby influencing the

accumulation/loss dynamics of soil organic matter stocks and ecosystem carbon dioxide efflux (Frey et al. 2013; Karhu et al. 2014). CUE is therefore an important concept for understanding the future trajectory of soil-climate feedbacks, recognition of which has led to recent reviews of the topic (Manzoni et al. 2012; Sinsabaugh et al. 2013), application in ecosystem models (Wang et al. 2013; Allison 2014; Wieder et al. 2014), and the development of new methods to estimate microbial efficiency in environmental samples (Blazewicz and Schwartz 2011; Dijkstra et al. 2011b; Herrmann et al. 2014). However, progress in this field is hampered by chronic issues symptomatic of a divide among research approaches and discipline-specific terminologies. A common, interdisciplinary framework is needed to unite these current perspectives.

The relevance of CUE spans scales ranging from a single microbial cell to entire ecosystems. For example, variation in CUE has been linked to substrate biochemistry (Linton and Stephenson 1978; Payne and Wiebe 1978; Lemee et al. 2002), thermodynamic and genetic capacity of the cell (Roller and Schmidt 2015), the environmental sensitivity of microbial physiology (Apple et al. 2006; Schipper et al. 2014), consumer-substrate stoichiometric balance (Creamer et al. 2014; Mooshammer et al. 2014), and microbial community structure and activity (Six et al. 2006; Blagodatskaya et al. 2014). Other approaches have meanwhile explored CUE from food web and ecosystem perspectives, such as the effects of altered efficiency on availability of resources to higher trophic levels [i.e., Lindeman's ecological efficiency (1942)] and the mediation of ecosystem services like C sequestration (Frey et al. 2013). CUE is thus increasingly recognized by microbiologists, ecologists, and modelers alike as essential for understanding the causes and consequences of microbial C cycling.

The drawbacks of such wide-ranging approaches to measure and interpret CUE become evident after only a brief introduction to the literature. Numerous habitat-specific (and even laboratory-specific) methods for quantifying CUE have emerged to accommodate the challenges of working within specific systems (e.g., pure cultures, soil, and water), yet rarely are these methods developed with cross-site synthesis in mind. The wide range of published efficiency estimates produced by these many techniques (Manzoni et al. 2012) suggests that methodological differences

and limitations remain underexplored (Sinsabaugh et al. 2013). Unstandardized and poorly defined terminology further compounds these problems by making methods, conceptual advances, and conclusions difficult to compare among studies. Collectively, these problems inhibit a more synthetic understanding of microbial contributions to C cycling that integrates evidence from cellular to ecosystem scales.

At its core, CUE reflects a collection of numerous processes (some physiological, others characteristic of community or ecosystem dynamics) that influence C metabolism across varying scales of time and space. We establish here a conceptual model that honors and organizes this existing complexity by conceptualizing CUE as a hierarchy of increasingly broad temporal and spatial drivers of efficiency. In doing so, our approach distills important aspects of CUE (i.e., techniques, vocabularies, published estimates) with the goal of enhancing the interpretation and application of CUE data. Specifically, we:

- (1) Synthesize the major processes that affect microbial metabolism of organic C at physiological and ecological scales using a standardized terminology.
- (2) Structure these processes into a unifying model of CUE such that three nested definitions emerge from the literature—CUE_{P(OPULATION)}, CUE_{C(OMMUNITY)}, and CUE_{E(COSYSTEM)}.
- (3) Review research directions that will advance our current understanding of CUE.

Synthesizing the physiological and ecological basis of carbon use efficiency

Many of the problems that prevent broader synthesis of CUE concepts into a comprehensive framework stem from confusion concerning the factors that influence efficiency and the terminology used to describe them. For example, 'assimilation' is a term regularly used synonymously with 'uptake' or 'biomass production' even though all are distinct physiological processes (described below). Here we outline the major processes essential to C metabolism (from initial substrate uptake through biomass synthesis and turnover) for an individual microbial cell using a consistent terminology (Fig. 1). Key terms are highlighted in bold text throughout the following discussion and are defined in Table 1. CUE is used here only

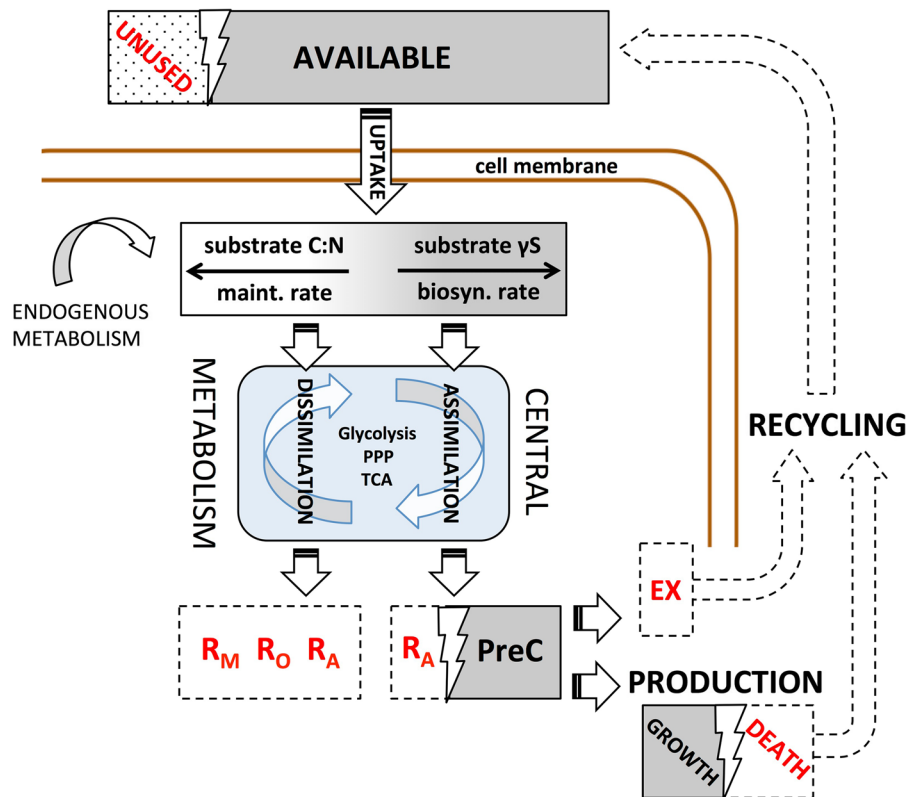


Fig. 1 Diagram of the carbon pools (*boxes*) and fluxes (*arrows*) associated with microbial metabolism. Substrate reduction (γS) and biosynthesis rate positively influence assimilatory demand, while substrate C:N and maintenance rate positively influence dissimilatory demand. Central metabolism is simplified as glycolysis, the pentose phosphate pathway (PPP), and tricarboxylic acid cycle (TCA). Maintenance (R_M) and overflow (R_O) respiration are prioritized during dissimilation; a transition to

respiration in support of anabolism (R_A) will occur if sufficient resources exist. Grey boxes represent pools of organic matter retaining the potential for use in growth; open boxes represent metabolic carbon losses from the cell (e.g., EX, exudates); stippling indicates organic matter unused for microbial uptake. Lightning bolts indicate pools divisible into subpools that may vary in relative size depending on soil and metabolic conditions (see text for further discussion)

in reference to that portion of C brought into the cell (i.e., uptake C) which a microorganism retains as microbial biomass. As a result, CUE is sensitive to extracellular forces that inhibit or promote recycling and reuse of microbial products and necromass but does not quantify stabilization of C outside the cell [e.g., humus yield; (Paustian et al. 1995)].

Uptake of substrates is the first step by which microorganisms internally process organic matter. Substrates are primarily directed towards central metabolism through the linked processes of glycolysis and the tricarboxylic acid cycle, although intracellular storage prior to metabolism is an alternative fate that remains poorly understood (Payne and Wiebe 1978; Frey et al. 2001). Assuming that a metabolic demand for carbon and/or energy exists, central metabolism

proceeds to either dissimilate or assimilate the substrate depending on various conditions (Neidhardt et al. 1990; Kim and Gadd 2008). **Dissimilation** maximizes the catabolic harvesting of energy and thus occurs preferentially when energy demands are high or energy limitation exists (Pirt 1965; Roels 1980; Gommers et al. 1988; Lemee et al. 2002; Fonte et al. 2013). Energy demands include non-growth maintenance activities (maintenance respiration, R_M) like motility, osmoregulation, and the molecular turnover of proteins and nucleic acids (Russell and Cook 1995; Wang and Post 2012). Nutrient limited cells also direct resources towards dissimilation; under these conditions, organisms mine organic matter via inefficient, carbon-spilling respiratory mechanisms (overflow respiration, R_O) in search of nitrogen, phosphorus, or

Table 1 Description of terms found in Fig. 1 and throughout this article

Term	Definition	Derivation	Measurement
Uptake	Amount of organic substrate taken up for microbial functioning, including respiration and biosynthesis	$\text{UPTAKE} = R_T + \text{EX} + \text{PROD}$	<p><i>Methodology</i> Measured change in organic substrate concentration external to biomass^a or inferred from sum of total respiration and production ($R_T + \text{PROD}$)</p> <p><i>Notes</i> Some portion of measured uptake may be substrate that “disappeared” due to any force preventing detection (e.g., sorption to mineral surfaces)</p>
Dissimilation	Complete substrate mineralization within central metabolism for the generation of energy equivalents	$\text{DISSIM} = R_M + R_O + R_A$	<p><i>Methodology</i> Respiration for maintenance requirements (R_M), during overflow metabolism (R_O), and to supplement anabolic (R_A) requirements^{b,c}</p> <p><i>Notes</i> DISSIM is the predominant pathway of carbon respiration during low biosynthesis and composes a diminishing portion of respiratory loss with increasing biosynthesis rates</p>
Assimilation	Partial substrate mineralization within central metabolism for the generation of energy equivalents, and partial generation of precursor (PreC) compounds	$\text{ASSIM} = R_A + \text{PreC}$	<p><i>Methodology</i> Respiration to support anabolism (R_A) of substrate^{c,d} and generation of precursor compounds used in biosynthesis^e</p> <p><i>Notes</i> ASSIM is the predominant pathway of carbon respiration during high biosynthesis as DISSIM (e.g., R_M) becomes a diminishing relative requirement^f</p>
R_T	Total carbon mineralized	$R_T = R_M + R_O + R_A$	<p><i>Methodology</i> Total respiratory losses, as measured by CO_2 production or O_2 demand^{g,h}</p>
PreC	Precursor carbon compounds generated during assimilation	$\text{PreC} = \text{EX} + \text{PROD}$	<p><i>Methodology</i> Metabolic flux analysisⁱ</p>
EX	Exudation of enzymes and other metabolites created from PreC	$\text{EX} = \text{PreC} - \text{PROD}$	<p><i>Methodology</i> Few methods exist for measuring exudation rates. Spectrophotometry has been used with cultured samples^j</p> <p><i>Notes</i> Synthesis of metabolites from PreC assumes no pre-existing biomass is used in metabolite generation</p>
Production	Gross biomass production, created using PreC	$\text{PROD} = \text{UPTAKE} - R_T - \text{EX}$	<p><i>Methodology</i> Short-term gross biosynthesis measured from changing cell densities^k or incorporation of (often) labeled carbon substrates (e.g., ^{13}C-glucose)^l, growth intermediates (e.g., ^3H-leucine)^{m,n}, or water (e.g. H_2^{18}O)^o</p> <p><i>Notes</i> Short incubation times avoid effects of biomass turnover, recycling, and other extracellular influences on net growth. By definition, gross production is greater than or equal to zero</p>

Table 1 continued

Term	Definition	Derivation	Measurement
Death	Turnover of biomass caused by many processes (e.g., microbivory, natural cell death)	$DEATH = PROD - GROWTH$	<i>Methodology</i> Direct measures lacking, although inferred from $(PROD - GROWTH)$ <i>Notes</i> By definition, death is greater than or equal to zero
Growth	Net biomass production	$GROWTH = UPTAKE - R_T - EX - DEATH$	<i>Methodology</i> Measurable using same methods as for PROD, but with longer period of observation <i>Notes</i> Long incubation times integrate effects of biomass turnover, recycling, and other extracellular influences on biosynthesis

Dissimilation refers to the catabolism of organic substrates in central metabolism strictly for the generation of energy equivalents (e.g., NADH, NADPH₂, ATP). Assimilation refers to the paired catabolism and anabolism of organic substrates in central metabolism for the generation of energy equivalents and the precursor carbon compounds (PreC) used in biosynthesis. Biosynthesis is the anabolic process of generating microbial biomass from PreC

^a Frey et al. (2001)

^b Manzoni et al. (2012)

^c Wang and Post (2012)

^d Gommers et al. (1988)

^e Kim and Gadd (2008)

^f Zhang and Lynd (2005)

^g Bott (2006)

^h Brant et al. (2006)

ⁱ Tang et al. (2009)

^j Kredics et al. (2000)

^k Keiblinger et al. (2010)

^l Frey et al. (2013)

^m Alden et al. (2001)

ⁿ Ward (2006)

^o Blazewicz and Schwartz (2011)

other nutrients (Russell and Cook 1995; Manzoni et al. 2008; Sinsabaugh et al. 2013; Creamer et al. 2014; Mooshammer et al. 2014). Finally, C may be dissimilated to support anabolic energy requirements for biosynthesis (anabolic respiration, R_A ; note the term “biosynthesis” is used throughout to describe the synthesis, polymerization, and assembly reactions that lead to creation of new biomass). CUE is theoretically zero during dissimilation as all C is ultimately respired, thus explaining the low CUE of organisms experiencing conditions of minimal growth, limited/poor quality resources, and nutrient stress.

Assimilation occurs under conditions more favorable to biosynthesis such as high resource quality or

nutrient abundance. Assimilation is characterized by both catabolic and anabolic processes that, respectively, generate the energy equivalents (anabolic respiration, R_A) and precursor carbon compounds (**PreC**) necessary for biosynthesis. These precursor compounds are siphoned away from central metabolism as pathway intermediates for incorporation into cell structures using the energy generated from both dissimilation and assimilation (Kim and Gadd 2008). Regardless of conditions, assimilation only occurs after non-growth requirements have been satisfied and sufficient excess C and energy are available (Dawes and Ribbons 1964; Ingraham et al. 1983; Kim and Gadd 2008). As a consequence, an increase in

assimilation and growth rates caused by increased substrate availability or the degree of substrate reduction positively affects CUE by reducing the relative amount of dissimilation needed to support maintenance. Assimilation has inherent respiratory losses (R_A), however, that limit maximum efficiency to ~ 0.85 for even the most reduced compounds (Gommers et al. 1988).

In summary, any environmental or biological factor that influences the relative amount of substrate assimilation or dissimilation will have a significant effect on CUE. Factors such as resource quantity and quality (e.g., C:N ratio, degree of substrate reduction) behave as “top-down” regulators by constraining the overall availability of energy and C, and thus the *potential* for biosynthesis. Meanwhile, a variety of “bottom-up” controls influence biosynthesis rates, and indirectly CUE, by affecting demand for PreC downstream of central metabolism (e.g., in organelles or cellular space where assembly of macromolecules occurs). For example, increasing temperature may increase efficiency by inducing assimilatory demand to sustain higher rates of biosynthesis (Pirt 1965; Linton and Stephenson 1978; Gommers et al. 1988) or, alternatively, decrease CUE if dissimilatory demands increase (Rivkin and Legendre 2001) because of higher rates of R_M (Marr et al. 1963). Maximum CUE should be achieved when both top-down and bottom-up forces work in concert, such as conditions where abundant, high quality resources are available and environmental cues (e.g., temperature, pH, community dynamics) are most conducive to biosynthesis.

Biosynthesis using precursor compounds produces new biomass, macromolecules to replace those that are degraded (i.e., molecular turnover), and a variety of metabolites destined for secretion (i.e., exudates; **EX**). Molecular turnover is traditionally considered a form of cellular maintenance while exudates like exoenzymes are considered a metabolic loss (Manzoni et al. 2012). Gross biomass production, on the other hand, is foundational to the concept of CUE when defined as the ratio of microbial production to the sum of production and respiration (del Giorgio and Cole 1998). Numerous processes occur beyond this stage of substrate breakdown, however, with important effects on CUE. For example, turnover of microbial biomass following cell **death** will reduce estimates of gross microbial production (defined here as **production**) into net production (defined here as **growth**). Extracellular recycling

of microbial necromass and exudates will then create feedbacks into the pool of available organic matter, thus making the interaction between recycled organic matter and the environmental matrix of water and/or minerals critically important (Bol et al. 2009; Grandy et al. 2009; Cotrufo et al. 2013).

Under certain conditions substrate availability cannot support biosynthesis and cell integrity can only be maintained by the metabolism of internal substrates like cellular proteins and nucleic acids or storage compounds. Endogenous metabolism can be significant in these cases (Russell and Cook 1995). The efficiency of an organism undergoing endogenous metabolism is largely unexplored, particularly regarding the transition between states of activity and dormancy that may be triggered by resource supplies. Such circumstances may well characterize a significant portion of microbial life history where resource availability is limited across space or time (del Giorgio and Cole 1998) and require further investigation. Our discussion also assumes that oxygen concentrations are optimum for microbial biosynthesis. Hypoxia may induce a shift from cellular respiration to generally less efficient fermentation (Pfeiffer et al. 2001; Lipson et al. 2009).

A unified conceptual framework for interpreting microbial efficiency

The preceding discussion reveals two specific challenges that influence how we interpret CUE data: the processes foundational to efficiency (1) vary in importance depending on the ecological scale of inference (population, community, ecosystem) and (2) become important at different stages of substrate breakdown. For example, short-term observations of CUE may emphasize the role of substrate uptake and maintenance respiration, while longer-term observations may be necessary to adequately capture the impact of substrate recycling. Because existing techniques for estimating CUE differ in the ecological and temporal scales they integrate, they often describe very different aspects of CUE. This could explain much of the variation in published CUE estimates that have been documented from culture-based, soil, and aquatic systems (Six et al. 2006; Manzoni et al. 2012).

Our conceptual model organizes microbial CUE as three nested definitions: CUE_P , CUE_C , and CUE_E (Fig. 2). Each of these terms is associated with

existing methods that estimate the influence of a unique suite of drivers on CUE at increasingly broad ecological scales. CUE_P describes the metabolic limits to carbon use efficiency intrinsic to a *population* of cells, most readily measured using pure cultures (Marr et al. 1963; Pirt 1965; Gommers et al. 1988). Naturally occurring aquatic or terrestrial microbial *communities* encounter additional drivers that may directly or indirectly affect CUE. CUE_C integrates these effects as the carbon use efficiency leading to gross microbial biomass production. Because methods for estimating CUE_C conventionally attempt to avoid factors that detract from gross production (e.g., biomass turnover), they are unreliable indicators of longer-term net stabilization of uptake C as microbial biomass. CUE_E is used here as the most inclusive definition of efficiency that incorporates *ecosystem*-scale forces controlling net dynamics of microbial biomass. Below we expand on these concepts and their relevance to researchers working in aquatic and soil systems using a variety of techniques.

CUE_P

Microbiologists in the 1950s adopted continuous-culturing (chemostat) techniques to closely examine species-specific CUE dynamics (Russell and Cook 1995). Efficiency is described in this context as the biomass yield from either a quantity of available catabolic ATP (Y_{ATP}) or mass of available substrate ($Y_{SUBSTRATE}$). These measurements, typically made under optimal biosynthetic conditions, can produce estimates of efficiency that approach theoretical maxima (Y_G , true growth yield; Pirt 1965) and are constrained only by thermodynamic and metabolic limits to efficiency. Combining a chemostat approach with isotopic enrichment (^{13}C metabolic flux analysis) can also provide estimation of metabolic PreC generation and biomass yield (Tannler et al. 2008; Tang et al. 2012). For pure cultures grown aerobically on non-limiting supplies of glucose, yield is typically ~ 0.6 , although higher estimates approaching ~ 0.85 have been observed for more reduced substrates and

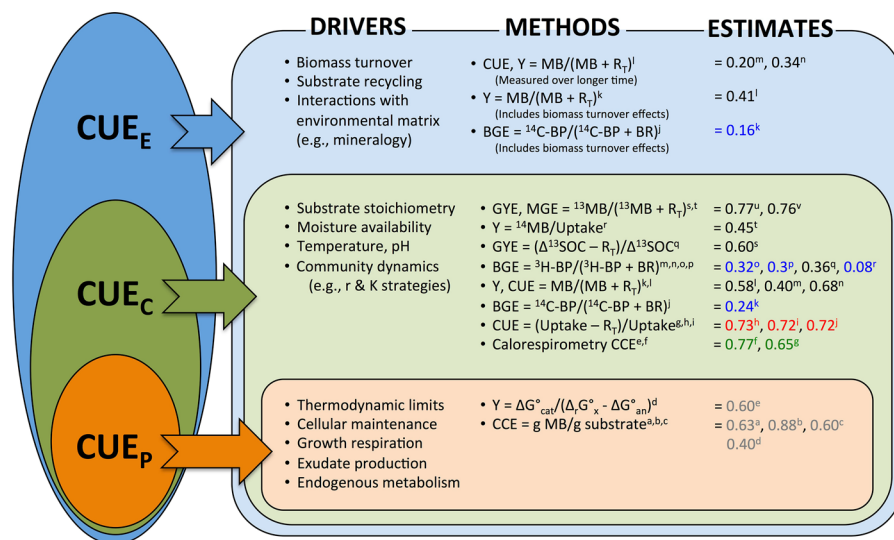


Fig. 2 The nested tiers of carbon use efficiency and the significant drivers at each scale of inquiry. Common methods and published estimates of efficiency associated with these levels are provided using the citing authors' original terminology in order to highlight the diversity of terminology used throughout the literature. Estimates are color coded by the type of sample analyzed: soil (black), water (blue), isotopologues in soil (red), calorespirometry in soil (green) and culture-based/thermodynamics (grey). CUE_P examples depict glucose (or similar) amendment. CUE carbon use efficiency, Y yield, MB microbial biomass, R respiration, BGE bacterial growth efficiency, BP bacterial production, BR bacterial respiration, MGE microbial

growth efficiency, SOC soil organic carbon, CCE carbon conversion efficiency, ΔG_{cat}^o , Gibbs energy of catabolism; ΔG_{an}^o , Gibbs energy of anabolism. ^aLinton and Stephenson (1978), ^bGommers et al. (1988), ^cBabel (2009), ^dTannler et al. (2008), ^evon Stockar et al. (2006), ^fBarros et al. (2010), ^gHarris et al. (2012), ^hDijkstra et al. (2011c), ⁱDijkstra et al. (2011b), ^jHagerty et al. (2014), ^kRam et al. (2003), ^lFrey et al. (2001), ^mBlagodatskaya et al. (2014), ⁿElliott et al. (1983), ^oApple and del Giorgio (2007), ^pKosolapov et al. (2014), ^qLee and Schmidt (2014), ^rOrtega-Retuerta et al. (2012), ^sThiet et al. (2006), ^tLipson et al. (2009), ^uBrant et al. (2006), ^vFrey et al. (2013). (Color figure online)

more efficient organisms (Linton and Stephenson 1978; Gommers et al. 1988; Babel 2009). Examining the efficiency of individual microbial species in situ is technically infeasible and so culture-based methods remain the standard for measuring carbon use efficiency of populations (CUE_P).

Important drivers of CUE_P include maintenance respiration rates, biosynthesis rates, and exudate generation. These can vary predictably by species, allowing classification of taxa as r- or K-strategists assuming a tradeoff exists between catabolic rate and yield (Angulo-Brown et al. 1995; Pfeiffer et al. 2001). Relatively rapid substrate utilization and biosynthesis rates would be a competitive advantage for r-strategists despite low overall CUE when conditions are C-rich; however, K-strategists would become favored when substrate is limiting. Bacteria and fungi have been broadly classified as r- and K-strategists, respectively, due to their anticipated average relative growth rates and CUE (Rousk and Baath 2007; Lipson et al. 2009; Keiblinger et al. 2010; Reischke et al. 2014), although efficient bacteria and inefficient fungi likely also exist. While CUE_P is a trait that differs among microbial species, it remains positively correlated with substrate availability and biosynthesis rate for any single species.

CUE_C

Although cultured laboratory populations have provided much valuable information regarding the physiological basis of efficiency, complex aquatic and soil microbial communities encounter many additional factors that influence CUE. These drivers include the bioavailability of C and energy (Linton and Stephenson 1978; Bremer and Kuikman 1994; Fonte et al. 2013), the sensitivity of growth rates to environmental fluctuations in, for example, temperature (Apple et al. 2006; Amado et al. 2013; Frey et al. 2013; Schipper et al. 2014), consumer-substrate stoichiometric balance (Rousk and Baath 2007; Creamer et al. 2014; Mooshammer et al. 2014), and microbial community dynamics (Six et al. 2006; Lipson et al. 2009; Blagodatskaya et al. 2014). Numerous approaches to measuring community-scale carbon use efficiency (CUE_C) exist using a ratio of biomass production and substrate uptake, where uptake can be approximated by the sum of production and respiration (Manzoni et al. 2012). These methods often employ

short-term incubations (often less than 3 h, but up to ~48 h) of a sample after amendment with an unlabeled (Devevre and Horwath 2000; Frey et al. 2001; Tiemann and Billings 2011) or isotopically-labeled substrate (e.g., ^{13}C -glucose, ^{14}C -acetate, ^3H -thymidine) (Fuhrman and Azam 1980; Cole et al. 1988; Alden et al. 2001; Brant et al. 2006; Dijkstra et al. 2011a; Frey et al. 2013). Given these shared characteristics, we use ' CUE_C ' as an umbrella term to organize all approaches that express the capacity for mixed microbial communities to utilize substrates for gross production over short periods before significant biomass turnover (Table 2). CUE_C thus eliminates the need for redundant terms like microbial growth efficiency, growth yield efficiency, yield, bacterial growth efficiency, and carbon conversion efficiency (Fig. 2).

CUE_C methods use relatively short incubations focusing on primary metabolism of a substrate before substantial recycling of necromass and exudates can occur. Indeed, isotopic labeling experiments have shown a rapid increase in the labeled portion of microbial biomass immediately after isotope amendment, followed by a stationary or declining phase (Brant et al. 2006; Blazewicz and Schwartz 2011; Reischke et al. 2014). These results suggest that isotopes track the initial generation and proliferation of nascent cells in the first hours post-amendment, followed by the net balance between production and biomass turnover over longer periods. Isotope-based techniques are generally preferable to unlabeled approaches because smaller substrate additions can be used that do not greatly enrich the available pool of organic matter. Labeled substrates also permit measurement of native soil organic matter priming, the mineralization of which would inflate respiration rates and underestimate CUE.

Based on the vocabulary developed here, the mathematical definition of CUE_C is (Eq. 1)

$$\begin{aligned} CUE_C &= \text{Production/Uptake} = (\text{Uptake} - R_T - \text{EX})/\text{Uptake} \\ &= \text{Production}/(\text{Production} + R_T + \text{EX}), \end{aligned} \quad (1)$$

such that CUE_C is the quotient of gross microbial biomass production and the sum of gross production, total respiration (R_T), and exudates (EX). Important aspects of this formula include (1) the inclusion of an EX term that is dependent on whether exudate

Table 2 A summary of characteristics distinguishing community-scale carbon use efficiency (CUE_C) from ecosystem-scale CUE (CUE_E). CUE_C primarily integrates drivers that result in gross biomass production before biomass turnover or any process that detracts from production. Conversely, CUE_E is a

measure of net biomass production (growth) reflecting all drivers of microbial efficiency, even those acting over longer time scales such as biomass turnover and recycling of necromass and exudates

CUE_C	CUE_E
Community-scale efficiency of microbial biomass synthesis	Ecosystem-scale efficiency of microbial biomass synthesis and recycling of necromass/exudates
$CUE_C = \frac{\text{gross biomass production}}{\text{substrate uptake}}$	$CUE_E = \frac{\text{net biomass production}}{\text{substrate uptake}}$
Ranges from 0 to 1	Ranges from 0 to 1
Ignores recursive dynamics of decomposition like biomass turnover and substrate recycling	Incorporates the effects of biomass turnover, substrate recycling, and organo-mineral interactions
Quantified by existing CUE methods ^a involving short (e.g., hourly) incubations after substrate amendment	Rarely measured, although quantifiable through use of longer incubation periods
Valuable for examining metabolic response of natural microbial communities to substrates over short time scales (hours)	Valuable as an ecosystem-level measure of carbon stabilization within microbial biomass over long time scales (days to months)

^a CUE methods here defined to include the most common substrate-based, growth rate-based, biomass-based, and uptake-based procedures. See Manzoni et al. (2012) for further description

generation is captured by the technique employed, and (2) CUE_C values range between 0 and 1, as gross production must be either zero or positive. A positive CUE_C is interpreted as the presence of production, while a value of zero indicates a lack of production. Although the calculation of CUE_C is the same as CUE_P , estimates of the former are generally similar or smaller in magnitude because of the suboptimal biosynthetic conditions likely to be experienced outside of pure culture (Fig. 2).

Interpretation of CUE_C values is critically dependent on time, specifically the sequential progression of processes that occur during substrate breakdown (Fig. 3). CUE_C should theoretically change with time following, for example, a pulsed organic matter amendment to reflect (1) an initial increase and peak in efficiency due to rapid uptake without substantial respiratory losses, followed by (2) a decline in efficiency due to accumulating C loss pathways (Eq. 1). Consequently, methods using very short incubation times are likely to overestimate CUE because they integrate uptake dynamics more so than complete metabolism (Nguyen and Guckert 2001; Hill et al. 2008; Sinsabaugh et al. 2013). On the other hand, incubations that are too long may integrate the effects of biomass turnover and substrate recycling. Accurate interpretation of CUE_C estimates therefore depends upon a relatively narrow window of incubation time

such that complete metabolism, but not substrate recycling, is captured.

CUE_E

The observation period of CUE_C methods leaves the ultimate fate of uptake carbon over time scales beyond the lifespan of an individual organism (days to weeks) undetermined. For instance, high CUE_C estimates may not necessarily translate to long-term C retention as microbial biomass under scenarios where biomass rapidly turns over and necromass is not readily recycled. A third definition of CUE becomes necessary in order to account for the drivers that become significant beyond the conventional incubation times of CUE_C . We propose an ecosystem perspective of carbon use efficiency (CUE_E) that integrates drivers originating from population and community scales, as well as time-dependent factors such as biomass turnover and the recycling of necromass and exudates that occur external to the cell. CUE_E is thus a measure of the efficiency of substrate retention as microbial biomass through biosynthesis (i.e., CUE_P and CUE_C) plus the efficiency of substrate recycling across generations of cells.

Because CUE_E integrates the effects of extracellular substrate recycling, the role of the extracellular environment becomes important at this scale. Microbial exudates and necromass are exposed to various

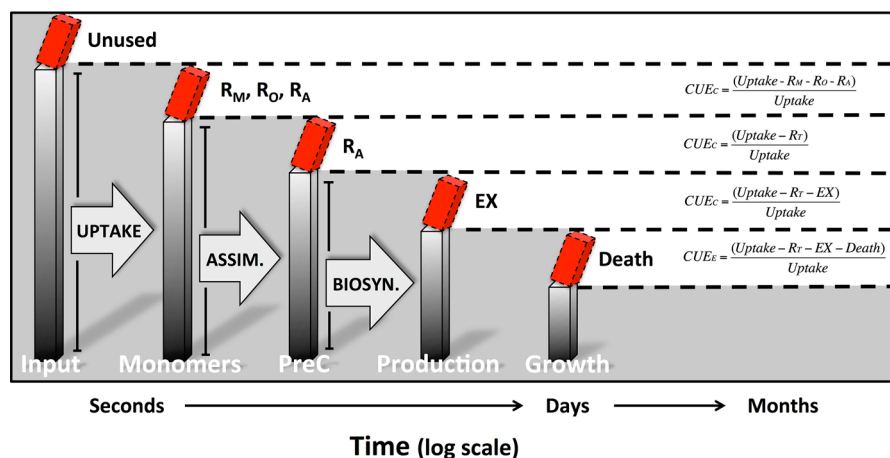


Fig. 3 Illustration of the accumulating loss terms that occur over time for a given unit of metabolized organic matter and the expected effect on carbon use efficiency (CUE_C , but also CUE_P). Boxes represent pools of carbon and arrows represent the transformations that convert carbon into new forms. For example, of the total theoretical input of carbon to a system, the cell will take up a portion while the balance remains unused. Of the carbon that is taken up by cell (now defined as monomers), a

portion is assimilated into precursor compounds (PreC) necessary for biosynthesis while the remainder is dissimilated as maintenance respiration (R_M), overflow respiration (R_O), or anabolic respiration (R_A). CUE declines as metabolism progresses and becomes CUE_E , or the net growth after time-dependent losses such as biomass turnover (Death). R_T total respiration; EX exudates

interactions with soil or sediment surfaces depending on soil texture and mineralogy (Fig. 1). These interactions may directly inhibit recycling by promoting formation of stable aggregates and organo-mineral associations, or can indirectly affect substrate stoichiometry through selective stabilization of some substrates, such as nitrogen-bearing compounds in clayey soils (Grandy et al. 2009; Cotrufo et al. 2013). CUE_E therefore depends on the uptake and metabolism of substrates that are likely changing in quality with time.

Using the terminology proposed here (Table 1), the mathematical definition of CUE_E is (Eq. 2):

$$\begin{aligned} CUE_E &= \text{Growth/Uptake} \\ &= (\text{Uptake} - R_T - EX - \text{Death}) / \text{Uptake} \\ &= \text{Growth} / (\text{Production} + R_T + EX). \end{aligned} \quad (2)$$

Important characteristics of this formula are that: (1) growth represents the *net* microbial biomass production resulting from all interacting ecosystem forces acting over space and time, and (2) CUE_E values can range between 0 and 1. The interpretation of CUE_E is significantly different from scales of CUE_P and CUE_C . A positive value suggests net accrual of uptake carbon as microbial biomass despite biomass losses, and zero indicates no uptake C remains in the microbial biomass pool.

Measuring microbial growth (net biosynthesis) is distinct from production (gross biosynthesis) in important ways. Short incubations (<3 h) following substrate addition more closely estimate microbial production, yet growth of the community could be zero for the same sample because of biomass turnover. Should CUE incubations be allowed to progress beyond the normal turnover time of microbes, techniques are more likely to reveal growth dynamics of the microbial community. Choosing an appropriate incubation duration that either captures or excludes biomass turnover and substrate recycling may be best decided from the average residence time of substrates in microbial biomass, or the average turnover rate of microbial cells. Hill et al. (2008) found glucose uptake to occur within 30 s of introduction but 6–8 h was the average residence time in microbial tissue. The average turnover rate of (soil) bacterial or fungal cells ranges from hours to days and from days to weeks, respectively (Rousk and Baath 2011). Incubations extending beyond 24–48 h are thus increasingly likely to reflect the effects of biomass turnover and substrate recycling on CUE estimates.

CUE_E values integrate all of the factors subsumed by CUE_C but also include the effects of cell death and the efficiency of necromass and exudate recycling. CUE_E estimates should thus be lower than CUE_C

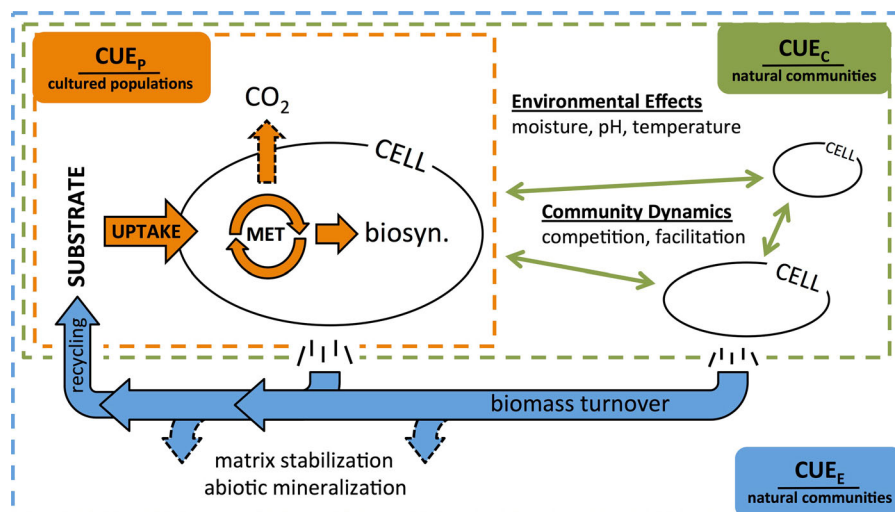


Fig. 4 Microbial carbon use efficiency partitioned into three nested definitions that integrate increasingly broad temporal and spatial drivers of efficiency. CUE_P reflects the species-specific functioning of microbial taxa (e.g., biosynthesis rate, exudate production) and thermodynamics of carbon substrate metabolism (MET) that limit the proportion of uptake carbon used for biosynthesis versus lost from the cell (e.g., mineralized or exuded as metabolites). CUE_P is generally measured on cultured populations. CUE_C is measured on natural (aquatic or soil)

communities and thus accounts for additional environmental and community drivers that affect microbial metabolism. Existing methodologies largely restrict CUE_C to reflect gross microbial production before recursive substrate recycling of necromass and exudates (*dashed lines* leading from cells). CUE_E describes long-term (e.g., days to months) carbon retention as net microbial growth due to CUE_P and CUE_C, but also the efficiency of substrate recycling among generations of cells

because these additional processes act to reduce microbial biomass production from gross to net values. For example, a discrete quantity of hypothetical organic C (e.g., from a pulse input of fine root tissue to soil, or an amendment of isotopically-labeled substrate) may initially be metabolized to yield a CUE_C estimate of 0.6 but become an apparent CUE_E of 0.4 upon cell death. This necromass may then interact with the extracellular environment, where recycling of substrates by neighboring cells must compete with processes like stabilization on mineral surfaces or aggregate formation that prevent their reuse. Even if all necromass and exudates are perfectly (100 %) recovered, however, respiratory losses will again result in C loss during each iterative round of metabolism (here by 40 %). This simplified scenario illustrates how CUE_E estimates must decline over time; indeed experimental evidence has shown reduced apparent CUE in the presence of microbial grazing (Frey et al. 2001; Ram et al. 2003) and over extended incubations (Elliott et al. 1983; Hunt et al. 1985; Blagodatskaya et al. 2014). CUE_E may ultimately approach zero as all of the hypothetical C is eventually lost from microbial biomass as respired

CO₂, humified stable organic matter, or been propagated up the food chain.

The declining pattern of CUE_E should not marginalize its value for understanding the many pathways and bottlenecks of microbial organic matter breakdown. The decline may occur over a period of days or decades depending on the net effect of substrate recycling and opposing processes like mineral stabilization, yet in either case vital information is at hand. For example, a CUE_E value that descends rapidly to zero with time may indicate quick biomass turnover and/or little capacity for substrate recycling because of strong organo-mineral interactions that restrict substrate bioavailability. Microbes under such a condition would require ample exogenous resources in order to remain at steady state biomass concentrations and may respire heavily or commit large amounts of necromass or exudates to a stable, biologically unavailable, organic matter pool. On the other hand, relatively high CUE_E values suggest a more “self-sustaining” microbial biomass that efficiently retains C within biologically active biomass pools. The biomass turnover and recycling dynamics inherent to an ecosystem perspective of CUE thus provide an

important perspective to the debate over how changing microbial CUE may affect global carbon stocks (Frey et al. 2013; Allison 2014).

Summary and future directions

We believe our conceptual model of CUE enhances the interpretability of existing estimates by drawing together, and creating order from, the biological and methodological components of various research perspectives (Fig. 4). Researchers may ultimately choose a CUE_P, CUE_C, or CUE_E approach to address a specific question, but must be cognizant of the inherent limitations that each possesses as intrinsic, absolute, and apparent measures of carbon use efficiency, respectively (Table 2). CUE_P estimates provide the most accurate indication of taxon-specific, genetically constrained physiological limits to metabolism that intrinsically affects CUE at any scale of observation. Alternatively, if the natural environmental and community effects on efficiency are of interest, a variety of CUE_C techniques using labeled and unlabeled substrates and calorimetry exist (Fig. 2). These approaches provide valuable measures of the absolute efficiency achieved by complex communities during metabolism of substrates immediately upon uptake, given existing conditions for biosynthesis. Importantly, these methods largely ignore the biomass turnover and substrate recycling that affect gross biomass production. The ecosystem perspective of CUE_E integrates all relevant drivers in order to describe the apparent efficiency of microbial processing of C that results from all interacting population, community, and ecosystem-scale constraints.

Microbial CUE will become a more broadly interpretable and easily communicated concept as efforts to synthesize available data are made and a standardized terminology is employed. We make the following suggestions to immediately and directly improve the collective conversation surrounding microbial efficiency.

- (1) *Use of consistent terminology* Foremost, a standard vocabulary regarding carbon use efficiency is necessary groundwork in order for discipline-specific findings to be both accessible and usable by the broader scientific community.

More careful use of language should be a particular concern in order to avoid miscommunication and confusion. Our conceptual approach uses well-defined terminology amenable to a range of research interests (Table 1) and we hope that future work will use these suggestions with an eye towards standardization. The terms CUE_P, CUE_C, and CUE_E also conveniently organize the important drivers of efficiency and the most commonly used methods by scale of inference (Fig. 2).

- (2) *Recognition of methodological assumptions* Researchers must be aware of the full breadth of assumptions and limitations inherent to various techniques, particularly when attempting to compare efficiency estimates that do not share the same methods. Unfortunately the full scope of assumptions associated with most methods is still unrealized, and thus only a “best guess” can be given as to what a particular efficiency estimate truly represents. For instance, whether exudate generation and biomass turnover have been accounted for will vary between techniques that differ in substrate incubation lengths. Careful choice of the proper experimental approach can help reduce the number of assumptions that often qualify results.
- (3) *Comparison of methods* A comprehensive experimental comparison of available techniques for measuring microbial efficiency has not been done. Thus, any variability in efficiency estimates produced by different methodological approaches should not be explained as due to ecological factors until inherent differences in methods have been fully explored. For instance, a recently described divergence in CUE for aquatic and terrestrial systems (e.g., ~0.3 and ~0.6, respectively) (Manzoni et al. 2012; Sinsabaugh et al. 2013) may be a biological consequence of how microorganisms perceive heterogeneous (soil) versus potentially more homogenous (aquatic) environments. Alternatively, aquatic methods may simply generate lower efficiency estimates because incorporation of substrates into proteins or nucleic acids infers direct biosynthesis by a cell (Alden et al. 2001), whereas methods applied to soils typically denote the broader process of

substrate uptake where internalized substrate may be used for biosynthesis or be passively stored (Payne and Wiebe 1978). The lack of a comprehensive methods comparison also perpetuates a culture of using only “in-house” techniques for measuring efficiency rather than objective choices among available methods. Methods transparency will better permit researchers to select the technique that best matches their particular scale of inquiry.

- (4) *Measurement of the extracellular forces shaping CUE_E* Many factors play a role in determining the ultimate proportion of metabolized C that becomes stabilized as microbial biomass. Beyond the short-term controls associated with microbial physiology, numerous properties such as exudate generation, biomass turnover, and substrate recycling become highly influential over time scales of days to months (Fig. 3). The mechanisms by which these factors influence efficiency are poorly understood and will require additional attention. For instance, at what rate are exudates produced under different biosynthetic conditions (Kawasaki and Benner 2006), and what is the long-term fate of these compounds? The regulatory control of soil or sediment mineralogy, or any environmental matrix, in making organic matter available for decomposition is an important yet underexplored step in CUE_E (Schmidt et al. 2011). Long-term radioisotope experiments have indicated that most substrate C is lost rapidly from soils in the first year of decomposition, but ~20 % may persist up to a decade later (Jenkinson 1968; Sorensen 1987; Voroney et al. 1989) as stable soil organic matter. Some organic matter is thus likely to remain subject to microbial processing and reprocessing for years.
- (5) *Use of CUE estimates in modeling* Simulation models of C cycling generally represent microbes implicitly by including static, time-invariant values of microbial efficiency that determine net C movement between pools after losses (Parton et al. 1987; Vallino et al. 1996). At this scale, efficiency is conceptually most closely related to CUE_E . However, CUE_E is a time-dependent system property that integrates a variety of processes. Given

this, it is unsurprising that ecosystem C models are sensitive to values of CUE and that so many reasonable but widely distributed recommendations exist for the appropriate estimates to use (del Giorgio and Newell 2012; Moorhead et al. 2012; Frey et al. 2013; Allison 2014). Moving forward, soil C models can avoid many of these concerns by explicitly representing microbial activity and the processes that cause ecosystem-level measures of CUE to diverge. Some are beginning to do this: the microbial-mineral carbon stabilization (MIMICS) model, for example, explicitly represents microbial C processing and incorporates efficiency values at the level of CUE_C (Wieder et al. 2014). Efficiency values in MIMICS are time-invariant, but the structure of the model allows for recursive processing of C through microbial biomass. Other recent models include efficiency parameters that conceptually match CUE_C but depict additional microbial processes like substrate recycling and dormancy not generally captured in CUE_C measurements [microbial-enzyme-mediated decomposition model, MEND (Wang et al. 2013); Extracellular EnZYme model, EEZY (Moorhead et al. 2012)]. Because CUE_E collapses all of the ecosystem-wide controls over microbial efficiency into a single number, it may not be valuable in explicit models where all drivers of CUE are individually represented. However, CUE_E measurements may serve to assess the accuracy of outcomes from such models.

- (6) *Collaboration* We hope that the framework proposed here will stimulate efforts for collaboration among researchers by providing a standard vocabulary and a means of interpreting efficiency estimates that come from dissimilar techniques and/or focus on different habitats. Collaboration will also encourage discussion about the merits of various approaches for quantifying efficiency and may lead to quicker methodological advancements. Many of the challenges and limitations discussed here will be best addressed through combined efforts from all of the disciplines that actively contribute to our understanding of microbial efficiency.

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Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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