Reviews and syntheses: Carbon use efficiency from organisms to ecosystems – Definitions, theories, and empirical evidence

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Abstract. The cycling of carbon (C) between the Earth surface and the atmosphere is controlled by biological and abiotic processes that regulate C storage in biogeochemical compartments and release to the atmosphere. This partitioning is quantified using various forms of C-use efficiency (CUE) – the ratio of C remaining in a system over C entering that system. Biological CUE is the fraction of C taken up allocated to new biomass. In soils and sediments C storage depends also on abiotic processes, so the term C-storage efficiency (CSE) can be used. Here we first review and reconcile CUE and CSE definitions proposed for autotrophic and heterotrophic organisms and communities, food webs, whole ecosystems, and soils and sediments using a common mathematical framework. Second, we identify general CUE patterns, such as the CUE increase with improving growing conditions, and apparent decrease due to turnover. We then synthesize >6000 CUE estimates showing that CUE decreases with increasing biological and ecological organization – from unicellular to multicellular organisms, and from individuals to ecosystems. We conclude that CUE is an emergent property of coupled biological-abiotic systems, and it should be regarded as a flexible and scale-dependent index of the capacity of a given system to effectively retain C.

1 Introduction

Carbon cycling is driven by biological, physical, and chemical processes – vegetation and phytoplankton take up CO_2 from the atmosphere and convert it to biomass, decomposers and animals convert organic C to biomass and release it as CO_2, and physico-chemical processes redistribute and store C. Many of these processes involve the 'conversion' of C from various sources into biological products – the efficiency of this biological conversion is generally referred to as C-use efficiency (CUE). Low CUE values imply that little C is converted to new biomass

relative to the amount consumed. As a result, less C is retained in the organism and more is released as CO_2 or other forms of C, in comparison to circumstances when CUE is high and the organism retains more C. In other words, from this perspective, low CUE is indicative of a more open biological C cycle. Therefore, understanding the degree of variation in CUE – especially along gradients of environmental conditions – is key for quantifying how much C is retained in biomass and potentially in an ecosystem in the long term (Allison et al., 2010; Manzoni et al., 2012). However, the connection between CUE and long-term C storage is complex, and mediated by multiple biological, ecological, and physical factors.

For biological systems (organs, individual organisms, or even entire communities), CUE is defined as the ratio between the amount of C allocated to new biomass and the amount of C taken up. While CUE defined in this way is a simple concept, interpreting its patterns of variation is not. CUE is in fact a property of the biological system under consideration, as it synthetizes in a single efficiency various biological processes occurring across a range of spatial and temporal scales (Geyer et al., 2016). In any organism, because the proportion of growth vs. maintenance respiration, the growth rate, and, more generally, the availability of C all vary in time, CUE is also expected to change. Any changes in environmental conditions that favour rapid growth will shift the balance of C allocation towards biomass production (or towards C storage) and away from respiration and other costs associated with the acquisition of resources (i.e., C losses in the organism mass balance), thus increasing CUE (Manzoni et al., 2017; Öquist et al., 2017; Vicca et al., 2012). Instantaneous responses to an environmental change may also differ from long-term responses involving acclimation and adaptation to the new conditions – both of which can potentially affect C allocation to different metabolic processes and hence CUE (Allison, 2014). In addition to responses to environmental change, metabolic processes also differ across levels of biological organization, leading to decreasing values of CUE as organisms become more complex and require more energetically-expensive structures (DeLong et al., 2010).

While the aforementioned mechanisms can be identified for individual organisms or uniform cultures, natural plant, microbial, and animal communities are composed of a number of different organisms whose metabolism may respond differently to environmental drivers. In addition, various interactions among organisms in an ecosystem lead to emergent patterns that are different from the sum of individual contributions. Therefore, by integrating the contribution of individual organisms with a range of different CUE values, patterns in community-level CUE may be different from those expected based on organism-level CUE (del Giorgio and Cole, 1998; Ettema and Wardle, 2002). For example, seedlings of conifer species can have a whole-plant CUE around 0.7 (Wang et al., 2015), but conifer forests encompassing a range of tree ages and species exhibit a CUE (defined as net primary productivity/gross primary productivity) of around 0.45 (DeLucia et al., 2007; Gifford, 2003). Similarly, ecosystem level CUE (defined as net ecosystem productivity/gross primary productivity) emerges from linkages between plants and decomposers and the way both communities process and exchange C (Bradford and Crowther, 2013; Sinsabaugh et al., 2017). Because at the ecosystem level CO_2 is released by both autotrophs and heterotrophs, ecosystem CUE values are lower than those of plant communities.

While variability in biological and ecological processes affects CUE at organism-to-ecosystem levels, the efficiency of long-term C storage in ecosystems depends on how much C enters physically protected or chemically recalcitrant compartments or is removed from the system by abiotic processes. The more C is removed via, e.g., leaching and lateral transfer in solution or to the atmosphere (Chapin et al., 2006; Cole et al., 2007), the lower the C-storage efficiency (CSE) of an ecosystem. The term CSE is used here instead of CUE to emphasize

that C storage in soils and sediments depends also on abiotic processes that do not 'use' C for their fitness in a manner similar to organisms, or on incomplete C turnover due to hampered heterotrophic activity. Moreover, as C is recycled in the soil or sediment system and progressively more C is lost, C accumulation becomes more
85   dependent on physico-chemical protection mechanisms that reduce accessibility of C to the decomposers and removal processes (Schmidt et al., 2011; Canfield, 1994; Mendonça et al., 2017; Stewart et al., 2007).

From these examples (and others that will be presented in the following), it is clear that CUE (or CSE) should be regarded as a flexible quantity that emerges from the underlying biological and abiotic processes at various spatial and temporal scales. Understanding to what degree CUE is stable or variable across scales is
90   important for correctly partitioning C in biogeochemical models, in which these efficiencies are sometimes assumed constant (e.g., microbial CUE), and in other cases are the result of modelled C fluxes. Measured CUE and CSE thus offer an opportunity for testing the capacity of models to describe how C is partitioned among different pathways, rather than to capture C fluxes.

With this aim in mind, we synthesize the numerous definitions of C-use and C-storage efficiencies
95   currently employed across levels of biological and ecological organization and spatial-temporal scales, and develop a coherent mathematical framework for these different definitions. Next, we analyse how these efficiencies vary across scales and levels of organization, and how at the whole-ecosystem level, physico-chemical processes that lead to stabilisation or incomplete turn-over of organic matter become relevant to evaluate C retention. While previous syntheses have investigated the drivers of CUE patterns in specific systems (Canfield,
100   1994; del Giorgio and Cole, 1998; DeLucia et al., 2007; Manzoni et al., 2017; Sinsabaugh et al., 2015; Sterner and Elser, 2002), we focus here on scale-dependencies of CUE and CSE across systems, and discuss the limitations that arise in the interpretation of efficiency values due to these scaling issues. Finally, we discuss the relevance of the trends we find in relation to our understanding of the C cycle, for informing ecosystem model development, and for overcoming disciplinary boundaries that led to numerous conceptually similar CUE
105   definitions.

2 Theory

2.1 General carbon balance equations and definitions of C-use and C-storage efficiencies

In this section, general equations are presented to define C-use and C-storage efficiencies (CUE and CSE, respectively). We use the term CUE for efficiencies that are relevant for biological systems (from individuals to
110   communities), in which C is actually 'used' for functions related to the organism or community fitness. In contrast, systems in which both biological and abiotic storage processes occur do not literally 'use' C, but 'store' it and thus the term CSE will be used instead of CUE. The term 'storage' is used instead of 'sequestration' because we do not focus on the long-term stabilization of C, but only on the efficiency of C retention in relation to C inputs. All symbols are defined in Table 1.
115   For a generic C compartment representing an individual organism or a whole ecosystem with clearly defined boundaries, a general mass balance equation can be written in the form

$$\frac{dC}{dt} = I - O, \tag{1}$$

where C is the amount of C in the compartment, and the balance of inputs I and outputs O determine the rate of change of C. Inputs and outputs typically depend on external environmental factors and internal state variables, and are defined differently for organisms and ecosystems, as discussed in the following. In this general equation,

120 changes in stored C can be linked to the rate of C input. This linkage represents a simple definition for an 'apparent' C-use efficiency (CUE_A; we use this term for convenience, noting that CSE_A should be used for systems involving abiotic C exchanges) – the ratio of C remaining in the system (i.e., $\frac{dC}{dt}$) over C added to the system (I). This is an 'apparent' efficiency because it is calculated solely from C input and change in storage, without any consideration of the underlying processes that determine the C outputs. As will become clear, this pragmatic

125 definition is insufficient for CUE to have a biological meaning. Based on this definition, Eq. (1) can be recast as

$$\frac{dC}{dt} = CUE_A \times I, \tag{2}$$

where CUE_A describes the fraction of the input that ends up in C. Expanding the definition of CUE_A using the mass balance Eq. (1), CUE_A can be also defined in terms of input and output rates,

$$CUE_A = \frac{dC/dt}{I} = 1 - \frac{O}{I}. \tag{3}$$

These two equalities allow estimating CUE_A from measured changes in C pool size and C exchange rates. Hence, the apparent CUE is a dynamic quantity that depends on the ratio of output to input rates, or the ratio of change

130 in storage and input rate. For systems in which inputs are larger than outputs, $0 < CUE_A < 1$. In contrast, when outputs are larger than inputs, the system loses mass and $CUE_A < 0$. For biological systems where C represents the biomass of the organism (in C units), CUE_A represents the fraction of C uptake contributing to a biomass increase. For whole ecosystems, CSE_A is the fraction of C inputs via photosynthesis and physical transport contributing to C storage in vegetation and soils or sediments (Alin and Johnson, 2007; Canfield, 1994; Stewart

135 et al., 2007).

2.2 Carbon balance and efficiency equations for biological systems

Eq. (3) is not particularly useful to describe how effectively an organism uses C because it does not provide much mechanistic insight into the processes leading to the allocation of C to storage or output rates. However, Eq. (3) is used to estimate CUE in many practical applications where input and change in storage or input and output are

140 measured. If the observational setup is such that changes in storage and output rates can be unambiguously attributed to certain processes (e.g., gross growth and respiration), then the apparent CUE estimated from Eq. (3) is also a useful measure of CUE for that organism. However, in general, a more accurate description of the organism C balance is required to define a biologically meaningful CUE.

Let us now focus on C compartments representing the biomass (in C units) of an individual organism or

145 of a community. Here, 'organism' indicates any living entity, ranging from unicellular to multicellular, and from autotrophs to heterotrophs; regardless of their physiology and size, they are all treated as a C compartment with a well-defined boundary that allows defining inputs and outputs. In this context, the input I represents C uptake or ingestion, and the output O represents the sum of egestion, respiration, exudation, and turnover (i.e., mortality and senescence) (Fig. 1). Distinguishing among these processes is motivated by the different time scales for respiration

150 (seconds to hours) and turnover (minutes to years) processes. A first step towards quantifying the efficiency of C conversion to biomass – a central goal in most C budget studies involving CUE calculations for biological systems

– requires separating egestion (EG), respiration (R), exudation (EX), and turnover (T) (Sterner and Elser, 2002), i.e., splitting the output rate as $O = EG + R + EX + T$. Egestion includes C that passes through the guts without being assimilated (faeces); for plants and microorganisms, $EG = 0$. The exudation term may include excretion of

155   C compounds such as extracellular enzymes and polysaccharides, and secondary metabolites in microbial communities (Manzoni et al., 2012; Azam and Malfatti, 2007), dissolved organic carbon (DOC) and mucus in animals and phytoplankton (Darchambeau et al., 2003; Azam and Malfatti, 2007), and rhizodeposits (Hutsch et al., 2002) or C export to symbionts (Hobbie, 2006) in plants. Using these definitions, the C balance Eq. (1) can be re-written in more biologically meaningful terms for an individual organism or community as (Fig. 1),

$$\frac{dC}{dt} = U - EG - R - EX - T = G - T, \tag{4}$$

160   where U is the input (uptake) rate, G is the net growth rate in C units. This equation can be further re-written in terms of three measures of C conversion efficiency (Fig. 1) (Sterner and Elser, 2002): i) assimilation efficiency (AE $= (U - EG)/U =$ assimilation/uptake), ii) net growth efficiency (NGE = net growth/assimilation), and iii) gross growth efficiency (GGE $= AE \times NGE =$ net growth/uptake). Because our definition of CUE is conceptually equivalent to GGE, the acronym CUE is used in the following. Using these definitions, Eq. (4) is rewritten as,

$$\frac{dC}{dt} = AE \times U - R - EX - T = CUE \times U - T, \tag{5}$$

165   or equivalently (directly from Eq. (4)),

$$CUE = 1 - \frac{EG + R + EX}{U}. \tag{6}$$

The CUE can be regarded as a biomass yield or production efficiency, as it considers respired, egested, and exuded C as lost from the organism (Vicca et al., 2012; Payne, 1970; Manzoni et al., 2012; Geyer et al., 2016). Note that turnover does not affect CUE in Eq. (6). C storage compounds and osmolytes in this context are also regarded as 'biomass', as they would be measured as intracellular material. However, it could be argued that CUE should be

170   defined as $(G + EX)/U$ (Allison et al., 2010), because exudate synthesis has a clear fitness advantage that should be accounted for when defining a C-use efficiency. The difference between these two definitions of organism CUE is relevant when EX is large, as in the case of organic C exchanges between roots and plant symbionts (Hobbie, 2006); for microbial communities, the entity of the extracellular enzyme and polysaccharide synthesis is unknown but presumably small compared to the other rates involved (Schimel and Weintraub, 2003).

175   Respiration in Eq. (5) can be further broken down into growth (R_{growth}), maintenance ($R_{maintenance}$), and overflow ($R_{overflow}$) components activated when C cannot be used for growth or maintenance (Cannell and Thornley, 2000; Thornley and Cannell, 2000; van Bodegom, 2007; Russell and Cook, 1995). Hence, CUE can be expressed in terms of physiologically distinct respiration rates as,

$$CUE = 1 - \frac{R_{growth} + R_{maintenance} + R_{overflow} + EG + EX}{U}, \tag{7}$$

which demonstrates that any increase in the maintenance and overflow respiration rates relative to growth

180   respiration due to starvation or environmental stresses decreases CUE (Sect. 4.1). Similarly, CUE is expected to decrease when microorganisms invest in extracellular compounds (e.g., enzymes and polysaccharides) or plants support symbionts via exudation, due to increasing EX rate.

Unless biomass turnover can be neglected (in that case Eq. (2) and (5) are equivalent and CUE = GGE = CUE_A), combining Eq. (2) and (5) provides the relation between CUE_A and turnover rate,

$$CUE_A = CUE - \frac{T}{U}. \tag{8}$$

185   Based on this equation, higher turnover reduces CUE_A, but not CUE (Eq. (6)).

2.3 Carbon balance and efficiency equations for systems including abiotic components

We argued that CUE can be defined for biological entities that use C to improve their fitness, but that CSE should be defined for systems including abiotic components (or when organic matter turn-over is incomplete), for which fitness cannot be defined. Examples of such coupled biotic-abiotic systems are whole ecosystems (terrestrial and

190   aquatic), soils, and sediments, where different biological actors (primary producers, decomposers, herbivores, predators) mediate C cycling in association with abiotic processes such as C transport by advection (Chapin et al. 2006, Cole et al. 2007) and C-mineral interactions (Schmidt et al., 2011; Kaiser and Kalbitz, 2012). For these integrated systems, Eq. (1) should be expanded to include these processes (Fig. 2),

$$\frac{dC}{dt} = U + F_{in} - R - F_{out} = NECB, \tag{9}$$

where U and R represent respectively the C uptake and respiration rates by the biotic components of the system

195   (as in Eq. (4)), and F_{in} and F_{out} are respectively the C inputs and outputs occurring via abiotic exchanges of organic and inorganic C. With reference to ecosystems, the C balance of Eq. (9) can also be expressed in terms of the net ecosystem C balance, $NECB = \frac{dC}{dt}$ (Chapin et al., 2006).

        In analogy with Eq. (2) and using the rates defined in Eq. (9), the CSE for the whole system can thus be defined as,

$$CSE = \frac{NECB}{U + F_{in}} = 1 - \frac{R + F_{out}}{U + F_{in}}. \tag{10}$$

200   In a purely abiotic system ($U = R = 0$), Eq. (10) reduces to $CSE = 1 - F_{out}/F_{in}$. In contrast, when the abiotic C rates are negligible ($F_{in} \approx F_{out} \approx 0$), Eq. (10) reduces to $CSE = 1 - R/U = CUE$ – i.e., the C-use efficiency of the biological components in the system (analogous to Eq. (6) when C losses via respiration are dominant). Based on Eq. (10), any ecosystem storing C has CSE>0 (e.g., systems with long-term accumulation of C in undecomposed necromass, mineral-associated pools, or sediments).

205   Substituting the definition of CUE for the biological components into Eq. (10), an expression linking the system CSE and the biological CUE is found as,

$$(1 - CSE)(U + F_{in}) = (1 - CUE)U + F_{out}, \tag{11}$$

which essentially expresses the C losses from the system in two complementary ways – on the left hand side as the fraction of the total C input that is not stored, and on the right hand side as the fraction of the biotic C input that is not stored plus the abiotic losses.

210   **2.4 C-use and C-storage efficiencies in relation to empirical data**

Equations (6) and (10) provide general definitions of C-use and C-storage efficiencies, respectively for biological and coupled biotic-abiotic systems. The interpretation of these equations is straightforward when a 'control volume' is clearly identified that allows a meaningful empirical estimation of exchange rates and storage changes at the time scale of interest. For example, the body of an animal allows the identification of rates of ingestion,

215   respiration, exudation, and net growth that, taken together, close the biomass C balance equation. Even in this
conceptually simple case, however, cell turnover is not easily quantified. As such, net growth may be measured,
but not gross cell growth – and actually measuring these rates can be challenging. In most cases, defining and
separating input and output rates is even more complicated – both conceptually and practically when conducting
measurements. For example, closing the C balance of leaves, whole plants or plant communities, and aquatic

220   systems is challenging because both input and output fluxes are in the form of CO_2. Net exchange fluxes can be
readily measured, but not gross fluxes, complicating the separation of U (gross photosynthetic rate in this case)
and R (gross autotrophic respiration rate) – not to mention C exports to other parts of the plant. Other challenges
arise when separating autotrophic and heterotrophic contributions of respiration, but a single CO_2 flux is measured.
Common approaches for measuring C exchange rates relevant for CUE and CSE calculations are presented and

225   discussed in the Supplementary Information. We considered systems ranging from organism and communities, to
soils and sediments, food webs, and whole ecosystems and watersheds. A summary of CUE and CSE definitions
for these systems is presented and explained in Tables 2 and 3, and illustrated in Fig. 1 and 2.

3 Data collection and analysis

Estimates of CUE for a range of organisms (microorganisms, animals, and individual plants), communities

230   (microbial and plant) and ecosystems have been collected from the literature or calculated based on reported C
exchange rates (Table S1). Existing datasets or data collections shown in previous publications are used for CUE
of heterotrophic organisms (McNaughton et al., 1989; Manzoni et al., 2017), leaves (Atkin et al., 2015), plant
communities (Luyssaert et al., 2007), whole-terrestrial (Luyssaert et al., 2007) and aquatic ecosystems (Hoellein
et al., 2013), and for lacustrine and marine sediments (Alin and Johnson, 2007; Canfield, 1994). New literature

235   data collections are developed for CUE of microbial isolates, individual plants, non-vascular vegetation, food
chains, soils, and watersheds. The whole database encompasses nearly 6100 CUE estimates.

CUE values are recorded in our database as they are reported in the original publications, and thus reflect
variation in the environmental conditions (e.g., temperature, water availability) and organism status (e.g., actively
growing, energy- or nutrient-limited), as well as methodological confounding factors. The large majority of data

240   sets encompass independent data points obtained from different sites or treatments. Some time series are included
to illustrate how CUE values change during plant ontogeny or as resources are consumed in soil incubations (these
datasets are not included in statistical analyses requiring independent samples). One data set require the conversion
of energy-based to C-based fluxes to calculate CUE (McNaughton et al., 1989). Energy flux data [kJ/m^2/y] are
first converted to dry weights using animal and ecosystem-specific plant-community heat of combustion values

245   (Golley, 1961). Dry weights are finally converted to C-mass units assuming a conversion factor of 0.45 g C/g dry
weight.

The aim here is to illustrate the range of variation in CUE across spatial and temporal scales, and levels
of biological and ecological organization, and not to explain the observed variability. This latter goal would
require ancillary data on environmental conditions and physiological status that are not available in all studies.

250   Further, a comparison of CUE estimates across these diverse data sources is also challenging because of the
contrasting spatial and temporal scales at which measurements were conducted (Fig. 3). As such, and given our
aim, we have not attempted to scale up or down individual CUE estimates.

While it is not possible to quantitatively and statistically compare CUE estimates across all the scales involved due their different meaning, variations can still be interpreted as a result of scale differences. In subsets of the database in which CUE had been estimated in the original sources at consistent spatial and temporal scales, quantitative comparisons among the median values of each subset are possible, and are conducted using the Kruskal-Wallis test with a significance threshold set at p=0.05 (MathWorks, 2011). These subsets are: i) CUE of plant communities and ecosystems, and CSE of soils (plot-to-field spatial scale and annual scale), and ii) CUE of microbial isolates, soil microbial communities, and aquatic bacterial communities (sample size of a litre or less; time scales in the order of days). Moreover, we test with the same approach differences among the medians of smaller data groups within each subset.

For visual comparison, CUE data are grouped according to the subsystems shown in Fig. 2, and the distribution of the available CUE estimates is shown using box-plots. For each subsystem, some examples are extracted to illustrate specific CUE patterns, and the 90th percentile of each group is calculated to provide an indication of the maximum CUE that a sub-system can achieve.

4 C-use and C-storage efficiency patterns

Based on the theory outlined in Sect. 2, we present here examples on how measured CUE can be driven by 'true' biological factors that affect C partitioning in organisms, but it can also be affected by confounding factors such as biomass turnover rates (Sect. 4.1). We then present a synthesis and discussion of CUE trends along biological and ecological levels of organization (Sect. 4.2), across spatial and temporal scales (Sect. 4.3), and compare systems with and without abiotic transport processes (Sect. 4.4). Finally, we ask to what degree CUE estimates are useful for characterizing C allocation patterns and eventually informing C storage calculations and ecosystem models (Sect. 4.5).

4.1 Biological drivers vs. confounding factors of C-use efficiency at the organism and community levels

Various forms of C-use efficiency are used to characterize the fate of C inputs into a system. To this purpose, CUE is often estimated by measuring changes in C content of and C inputs to that system (Eq. (3)). If biomass turnover can be neglected, this 'apparent' CUE is a good approximation of the actual CUE (growth over C uptake ratio, see Eq. (8)), but in most cases biomass turnover is present and hard to quantify – in such a case, CUE_A estimates can be significantly lower than the actual CUE (Hagerty et al., 2014; Grossart and Ploug, 2001). Fig. 4a shows how apparent CUE is expected to decrease with increasing turnover rate in relation to C uptake (Eq. (8)). CUE_A values can in principle become negative when the turnover rate is higher than the growth rate (similar issues arise at the ecosystem and watershed scales, but due to C transport rather than turnover). Fig. 4b illustrates these effects by considering data from two studies on soil systems where turnover rate was manipulated. In the first study (Ladd et al., 1992), the ^{14}C initially added to the soil was taken up by microorganisms with a certain actual CUE, but as the incubation progresses, the ^{14}C remaining in the microbial biomass decreased partly due to cell turnover. As a result, CUE_A at the beginning of the incubation is higher than after about 100 days. It is also possible that during this period substrates became less available, leading to an increase in maintenance respiration compared to growth respiration (as discussed in the following). In the second example, biomass turnover was manipulated by controlling soil fauna feeding on soil microorganisms (Frey et al., 2001). When grazers were

290   active, the CUE$_A$ estimated from C accumulation into biomass was lower than in the samples without grazers. However, if CUE was calculated from changes in C substrate and respiration, estimates were insensitive to grazing pressure (Frey et al., 2001). Similarly decreasing CUE$_A$ has been found in aquatic bacteria subject to increasing grazing pressure (Grossart and Ploug, 2001). We therefore expect that for a given experimental setting, higher rates of mortality or predation will lead to lower estimates of CUE.

295   Figure 5 illustrates how changing the relative importance of maintenance costs (respiration and exudation) as compared to growth respiration alter CUE. Theoretical predictions are shown in Fig. 5a,b, where two methods often used in models to account for the metabolic costs of maintenance are considered (Thornley and Cannell, 2000). When growth respiration has priority over maintenance respiration, C required to sustain maintenance costs is obtained from the pool of assimilated C. In this case, CUE decreases linearly with increasing

300   maintenance costs and because maintenance can cause a net biomass loss, CUE can become negative (Fig. 5a). As an alternative, C required to fulfil maintenance costs can be directly deducted from the C uptake rate, before C is assimilated and thus before using C for growth respiration. In this case, CUE can at most reach zero, when all the C taken up is used for maintenance (Fig. 5b). Thus, both modelling approaches yield the same result that CUE decreases with increasing maintenance costs. Similar trends would appear if exudation was considered

305   instead of maintenance respiration, because mathematically these different C loss pathways have similar effects on CUE (Eq. (7)). Empirical evidence lends support to the prediction that maintenance costs decrease the overall CUE, whereas actively growing organisms in which growth respiration is dominant have higher CUE (Sinsabaugh et al., 2015; del Giorgio and Cole, 1998). This simplified view explains some, but not all observed patterns in CUE. For example, low-resource environments could select for high-CUE organisms despite low growth rates.

310   At the other end of the resource availability spectrum, to achieve high growth rates, it might be necessary to increase respiratory losses via C-overflow, futile cycles, and increasing costs of protein turnover, or due to the low energy content of the substrate being consumed. Thus, at very high G, a trade-off between growth and CUE may emerge (Lipson, 2015). Combining these pieces of evidence, CUE would be expected to first increase with increasing G, then reach a peak and decrease at high G values.

315   For example, the CUE of soil microbial communities tends to be low just after addition of a labile C substrate (lag phase, which can vary in length depending on the preceding physiological status), then to increase sharply as growth rate increases, and finally to decrease because microbes switch from a relatively efficient growth mode when substrates are available to a less efficient maintenance mode when substrates have been exhausted (Öquist et al., 2017) (Fig. 5c,d). Notably, when reductions in biomass occur under starvation conditions due to

320   conversion of biomass to maintenance respiration, CUE<0 (Fig. 5d). Similarly, plants maintain a high CUE until they stop growing vegetative tissues and shift allocation of resources to seed filling (Fig. 5e). In forests, CUE (defined as biomass accumulation over GPP; see Table 2) declines with decreasing nutrient availability (Fig. 5f). However, different from other examples in Fig. 5, this decline cannot be attributed to higher respiration under nutrient limited conditions, but rather to higher C investment to plant symbionts (Vicca et al., 2012). Because the

325   effects of higher maintenance respiration or exudation rate have the same direction – both decreasing CUE – we can expect that along resource or environmental gradients characterized by increasing maintenance costs (including exudation), CUE will decrease.

       A somewhat similar argument has been proposed to explain increases in CUE with increasing nutrient-to-C ratios of the resources used by heterotrophic organisms (Manzoni et al., 2017). High nutrient availability

330 with respect to C allows growth of the nutrient-rich cells typical of heterotrophs. However, under nutrient shortage and assuming that cell nutrient concentrations are relatively stable (homeostasis), resources contain C in excess, which can be selectively removed via overflow mechanisms (Russell and Cook, 1995; Boberg et al., 2008), increased C excretion (Anderson et al., 2005), and possibly C investment in extracellular compounds that promote resource availability (Middelboe and Sondergaard, 1993). As a result, C losses can become decoupled from

335 growth, leading to reduced CUE under nutrient shortage conditions (Manzoni et al., 2017).

4.2 C-use efficiency across levels of biological and ecological organization

We start from the C balance of leaves and move towards whole organisms, communities, food webs, and whole ecosystems to illustrate how CUE varies across levels of biological and ecological organization. The majority of C taken up by leaves is converted into products (CUE≈0.9, Fig. 6a), as might be expected for the organ responsible

340 for the entry of C into the biosphere. But while leaves must support their limited metabolic needs, whole plants require energy to maintain a range of additional functions that leaves do not, including nutrient uptake and use, regulation of ion balances and phloem transport, and excretion of C for symbionts (Cannell and Thornley, 2000; Thornley and Cannell, 2000). Thus, while leaf CUE is highly efficient, the cost of maintaining a complex organism reduces CUE from leaf-level values around 0.9 to whole-plant values of 0.6 (maximum CUE≈0.85). Similarly,

345 moving from unicellular to multicellular organisms requires additional C costs to maintain the structures of increasingly complex bodies (DeLong et al., 2010), resulting in a declining average CUE from approximately 0.5 (maximum CUE≈0.7) to 0.15 (maximum CUE≈0.5, Fig. 6b,e).

Comparing terrestrial bacteria and fungi, it has been suggested that they should differ in CUE, mostly due to their contrasting life histories (fast growing, inefficient bacteria vs. slow-growing, efficient fungi).

350 Although this paradigm has been around for some time, the hypothesis was not unequivocally supported (Thiet et al., 2006; Six et al., 2006). Recently, fungi and Gram-negative bacteria have been suggested as important biomarkers when evaluating CUE (Bölscher et al., 2016), but the link between the two is so far not clearly established. The collected CUE data for litter decomposers (arguably mostly fungi, at least in the first phases of litter degradation) suggest a lower CUE than in bacterial communities (Fig. 6b). However, litter decomposers in

355 forest ecosystems face strong stoichiometric imbalances and CUE estimates for these organisms represent long-term averages including periods of slow growth (Manzoni et al., 2017). These factors could explain the lower average CUE of litter decomposers and aquatic microorganisms compared to soil microorganisms and bacterial isolates – these patterns are thus driven by environmental effects, in addition to organism complexity *per se*.

Food webs include interacting organisms that exchange C among them and with the environment. Each

360 organism exchanges C according to its own CUE (for a modelling example, see Frouz et al., 2013b), but also provides C to the next organism (consumer or predator) in the food web. CUE (or more appropriately C transfer efficiency) defined as the growth rate of a target organism over the rate of C entering the food web (Sect. 1.5 in the Supplementary Information) is then expected to be lower than the CUE of the constituent organisms, as C is lost at each step in the food web, as shown in Fig. 6e. Moreover, antagonistic interactions in a food web may

365 increase metabolic costs, also lowering CUE (Toljander et al., 2006). Similar to the organism-level responses to resource availability, also food web efficiencies tend to be higher in resource-rich environments. For example, the fish-to-phytoplankton production ratio is higher in nutrient-rich conditions (Dickman et al., 2008). In soils, a food web developing on low C:N litter can be more efficient at retaining C in the system than one developing on high

370 C:N litter, despite no observable difference in C input (Frouz et al., 2013a). In the latter example, it is important to emphasize the role of soil fauna in mediating this response to nutrient availability – the presence of macro-fauna facilitates (via bioturbation) the transport of C towards sites where it can be stabilized.

Like moving from simple towards more complex organisms or interacting organisms in food webs, also considering whole ecosystems results in lower C retention capacity compared to individual organisms and communities. Aggregating processes results in lowering CUE for a given GPP, in particular when adding more 375 heterotrophic components (Fig. 2). Including the contribution of heterotrophic respiration is expected to decrease ecosystem CUE compared to vegetation CUE because more of the C taken up by plants is returned to the atmosphere (Fig. 7; Eq. (4) in the Supplementary Information). The CUE of vascular plant communities is indeed significantly higher (CUE≈0.42) than that for ecosystems (CUE≈0.19), which in turn is significantly higher than the soil C storage efficiency (on average slightly above zero).

380 We can also ask how the CUE of the ecosystem components affect the overall ecosystem CUE. It could be argued that with more efficient organisms, the ecosystem-level CUE would increase. This would be correct only if organisms merely acted as passive storage compartments in series, while some organisms – notably decomposers – alter the kinetics of decomposition via extracellular enzymes that are thought to be produced in proportion to the live biomass (Schimel and Weintraub, 2003). As a result of these feedbacks, it is possible that 385 lower (rather than higher) decomposer CUE increases ecosystem CUE and thus C storage potential, as indicated by empirical (Kyaschenko et al., 2017) and modelling studies (Allison et al., 2010; Baskaran et al., 2017).

Comparing aquatic and terrestrial systems, ecosystem CUE and soil or sediment CSE exhibit contrasting patterns. While the CUE of aquatic ecosystems is significantly lower than that of terrestrial ecosystems (Fig. 6c), the CSE of lacustrine and marine sediments is significantly higher than that of soils (Fig. 6d). The first pattern is 390 explained by allochthonous C contributions to respiration (Sect. 4.3), whereas the higher CSE of sediments can be explained by the often high sedimentation rate (Calvert et al., 1992) and the relatively short oxygen exposure time of organic C after burial (Canfield, 1994; Hedges et al., 1999), whereas most soils remain aerobic and C storage capacity may saturate (Stewart et al., 2007). Indeed, paddy soils where respiration is low due to anaerobic conditions store C more efficiently (median CSE=0.07) than other agricultural soils (median CSE=0.02; p<0.05). 395 Moreover, physical losses from soils (leaching, erosion) are probably larger than for sediments, at least in stable depositional environments.

Based on these analyses we can conclude that increasing the level of biological or ecological organization generally implies a more open C cycle – this is caused by increasingly costly structures to maintain complex organisms, and by increasing heterotrophic contributions when assessing the C storage potential of ecosystems as 400 opposed to vegetation alone.

4.3 C-use efficiency across spatial and temporal scales

Moving up spatial and temporal scales involves integrating C exchange rates in space and time. In turn, integrating these exchange rates essentially averages out the contributions at the smaller or shorter scales by considering a larger number of organisms (e.g., populations vs. individuals) or species (communities vs. populations), a larger 405 spatial domain, and longer periods of time. This averaging effect generally leads to lower CUE than at the smaller scales. As shown in Fig. 3, CUE is estimated over a range of spatial and temporal scales depending on the system of interest, which requires us to interpret CUE in the light of averaged C exchange rates at these scales.

Because organism-level CUE estimates are biased towards actively growing individuals often isolated in highly controlled conditions, spatial averaging in field conditions that also includes inactive or slowly growing

410   individuals results in lower population- or community-level CUE. In the case of plants, CUE of individuals is on average around 0.62, whereas in plant communities CUE≈0.42 (Fig. 6a). Quoting Gifford (2003), "The difference may be an expression mostly of the impact of recurring stresses and resource limitations and the much greater average age of plants in the forests than in the controlled environments. Presumably the respiratory requirement for acquiring water and nutrients is lower when they are abundantly available." (p. 179-180). Moreover,

415   antagonistic interactions within communities might increase C costs (Toljander et al., 2006). This contrast between CUE estimates at individual and community scales is not apparent when comparing CUE of microbial isolates and soil microbial communities, which are not statistically different (CUE≈0.45, Fig. 6b). However, CUE of aquatic microbial communities from our dataset is significantly lower than that of microbial isolates (CUE≈0.25), despite the occurrence of high values in some communities (del Giorgio and Cole, 1998). The high

420   CUE of soil microbial communities could be due to generally higher resource availability in soils than in aquatic environments, or to amending soils with labile compounds that stimulate microbial activity and mask the contribution of slow-growing organisms to the sample's metabolism (Sinsabaugh et al., 2013). Moreover, it is plausible that individuals competing for limited resources and facing antagonistic interactions invest more C in resource extraction and defence than isolated individuals, resulting in lower microbial community CUE than

425   population-level CUE.

Integrating C exchange rates through time also tends to lower CUE with respect to short-term measurements often conducted after adding labile substrates to heterotrophic systems (Fig. 5c), or during active growing periods for plants (Fig. 5e). Instead, long-term CUE (assuming biomass turnover is correctly accounted for) includes periods of slow growth due to unsuitable environmental conditions, during which maintenance costs

430   and resource acquisition costs remain high while growth stagnates. As mentioned in Sect. 4.2, this could explain why long-term CUE of litter microorganisms is lower than the microbial CUE in other systems (Fig. 6b).

4.4 Interpreting C-use and C-storage efficiencies in systems with abiotic C fluxes

Transport processes can decouple local GPP from ecosystem respiration by feeding heterotrophs with allochthonous C or removing products of primary productivity before they enter the decomposition and herbivory

435   pathways. Allochthonous C can cause relatively large respiration losses even with low inputs from GPP (Duarte and Prairie, 2005; Hoellein et al., 2013), resulting in low or negative values of CUE when defined as NEP/GPP; a more useful definition of CUE should account for allochthonous C inputs, which are however seldom measured (Eq. (5) in the Supplementary Information). This pattern is apparent when comparing the CUE of terrestrial and inland aquatic ecosystems (Fig. 6c) – the former being predominantly positive, the latter being most often strongly

440   negative. Despite inland systems having negative ecosystem CUE due to large allochthonous inputs, marine systems can act as C sinks due to long-term storage in sediments (where C storage in the range 0.01-0.4% of net primary productivity; Seiter et al. (2005), Falkowski (2014)) and as dissolved inorganic C.

Physical removal of C also alters the estimated CSE. Because removing C reduces the C that can be stored for a given respiration rate, CSE decreases with increasing abiotic losses of C. When in addition to

445   respiration, these losses of C are considered, CSE decreases with respect to the ecosystem CUE estimated from biological fluxes, as shown at the ecosystem- and watershed-scale respectively by Eq. (5) and (6) in the

Supplementary Information. Using the few available watershed-scale studies where C losses via leaching and subsequent advection in surface water bodies were measured, we can compare CSE estimates with and without the contribution of abiotic lateral C losses. When only the biological components are considered, we found an

450 average ecosystem CSE=0.137, whereas including abiotic losses CUE=0.104 – i.e., a >30% reduction in storage efficiency. Similarly, in marine systems the export of particulate C from the euphotic zone by particle sinking lowers the potential efficiency of C storage in that zone, while allowing long term storage in the sediments (Dunne et al., 2005).

4.5 Do we need C-use efficiency estimates?

455 The practical difficulties in estimating CUE at various scales, and the inherent conceptual challenges with its multiple definitions beg the question as to whether it is useful to even discuss CUE. On one hand, there are theoretical and conceptual advantages for using CUE as a 'macroscopic' parameter characterizing organism or ecosystem metabolism – even without quantifying the underlying drivers (specific metabolic pathways, or detailed input and output rates). On the other hand, full process understanding requires identifying these drivers and in

460 such a case, CUE is merely the result of their combination, and knowledge of CUE values alone would be of little use.

The CUE is less variable than the rates of C exchange that define it and therefore allows comparing systems characterized by very different C exchange rates. For example, respiration and growth rates of microbial communities roughly double every 10 °C increment in temperature, whereas CUE changes much less – ranging

465 from a 25% decrease for every 10 °C temperature increment (Frey et al., 2013) to no change at all (Dijkstra et al., 2011), depending on the CUE estimation method. Relatively stable efficiencies are particularly useful for modelling purposes, as they allow 'closing' otherwise open (undetermined) mass balance equations. Similarly, while NPP, GPP, and ecosystem respiration vary by two orders of magnitude across biomes (Fernandez-Martinez et al., 2014), CUE values are relatively more constrained (if we exclude ecosystems with negative NEP).

470 Moreover, non-dimensional numbers such as CUE and CSE emerge as key drivers of system dynamics (Vogel, 1998; Buckingham, 1914). For example, CUE appears in stoichiometric equations describing nutrient fluxes in relation to C fluxes (Manzoni et al., 2010; Sterner and Elser, 2002). In these stoichiometric models, it is often not necessary to distinguish among various respiration components or to define specific kinetic laws for C exchange rates – a single 'macroscopic', lumped CUE parameter is sufficient to describe the balance of growth

475 and respiration. However, if CUE varies through time or in response to environmental conditions in complex ways, the advantages of having a single lumped parameter may be overcome by a cumbersome parameterization to describe these effects.

A similar issue arises when implementing biological processes that could result in variable CUE into models of soil biogeochemical processes (Allison et al., 2010; Frey et al., 2013), the marine C cycle (Dunne et

480 al., 2005), or vegetation dynamics (Huntingford et al., 2017; Smith et al., 2016). These models differ widely in the way they parameterize the C cycle. For some components of the ecosystem, certain models assume constant CUE values (e.g., CUE of microbial decomposers), whereas for others, more detailed descriptions are employed, resulting in flexible CUE (e.g., separating respiration components in vegetation) (Gifford, 2003). Clarifying patterns of variation in CUE thus helps define when CUE is indeed stable or, in contrast, when additional processes

485 driving variable CUE must be accounted for in models. For example, if soil biogeochemical models are

parameterized using microbial CUE values obtained from laboratory incubations, erroneous predictions could be made if those incubations are not representative of soils in natural conditions. Apart from possible scale mismatches between empirical estimates of CUE and model interpretation, models assuming a stationary set of metabolic responses could underestimate C retention. This is the case when CUE acclimates and buffers the

490 consequences of climatic changes by reducing C losses from the biosphere. In contrast, if changes in CUE amplify biosphere responses – e.g., due to selection of inefficient early-successional species – these models might underestimate potential positive feedbacks between the biosphere and global climate.

5 Conclusions

We have synthesized definitions of and explored variations in the efficiency of C use by organisms, communities

495 and ecosystems, and in the efficiency of C storage in soils and sediments. This synthesis highlighted conceptual similarities in the way these efficiencies are defined across disciplines, and some common interpretation issues. Despite the occurrence of confounding factors that can bias CUE and CSE estimates, we argue that these efficiencies can still be useful to compare systems where variations in C exchange rates are large. Because CUE and CSE are outcomes of a wide spectrum of processes, they are expected to be flexible and to respond to both

500 biological (e.g., trends in growth vs. respiration) and physical controls (e.g., C transport and environmental conditions) – as such, they are useful indices of changes in the C cycle through time and space and could be employed to benchmark short- (in the case of CUE) and long-term predictions (CSE) of soil and ecosystem models. By focusing on the conversion of C into new products rather than on C fluxes *per se*, CUE and CSE patterns offer alternative insights on the inner workings of the processes regulating the C cycle.

505 **Data availability**

Should the manuscript be accepted, the datasets supporting the results that are not already available in public repositories will be archived in the open-access database of the Bolin Centre for Climate Research (https://bolin.su.se/data/).

Author contribution

510 This work was designed by all the authors during two workshops. SM led the writing of the manuscript and prepared the figures; SM, PČ, PP, MT, MW, and GV collated and analysed data from the literature; all authors contributed to locating literature sources, discussing the content, and writing the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

515 **Acknowledgements**

Funding was provided by the Bolin Centre for Climate Research (Research Area 4), through the project "Scaling carbon-use efficiency from the organism- to the global-scale", and by the Swedish Research Councils, Formas

(grant 2015-468 to BL and SM) and Vetenskapsrådet (grants 2016-04146 to BL and SM, 2016-06313 to SM, and
621-2014-4266 to CB). HS acknowledges MEYS CZ grants LM2015075 and EF16_013/0001782 – SoWa
520   Ecosystems Research, and DAW acknowledges support from an NSERC Discovery Grant. We also thank all site
investigators, their funding agencies, the various regional flux networks and the FLUXNET project, for support
to the development of the database "Global Forest Ecosystem Structure and Function Data For Carbon Balance
Research" (Luyssaert et al., 2009).

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Table 1. Definition of symbols and acronyms.

Symbols and acronyms	Description	Dimensions *
AE	Assimilation efficiency	-
EG	Egestion	M L^{-2} T^{-1} or M T^{-1}
EX	Exudation	M L^{-2} T^{-1} or M T^{-1}
F_{in}	Abiotic carbon input	M L^{-2} T^{-1}
F_{out}	Abiotic carbon output	M L^{-2} T^{-1}
I	Input	M L^{-2} T^{-1} or M T^{-1}
C	Carbon-mass	M L^{-2} or M
G	Growth	M L^{-2} T^{-1} or M T^{-1}
CSE	Carbon-storage efficiency	-
CUE	Carbon-use efficiency	-
CUE$_A$	Apparent carbon-use efficiency	-
GGE	Gross growth efficiency	-
GPP	Gross primary productivity	M L^{-2} T^{-1}
NECB	Net ecosystem carbon balance ($= dC/dt$)	M L^{-2} T^{-1}
NEP	Net ecosystem productivity	M L^{-2} T^{-1}
NGE	Net growth efficiency	-
NPP	Net primary productivity	M L^{-2} T^{-1}
O	Output	M L^{-2} T^{-1} or M T^{-1}
R	Respiration	M L^{-2} T^{-1} or M T^{-1}
R_a	Autotrophic respiration	M L^{-2} T^{-1} or M T^{-1}
R_{growth}	Growth respiration	M L^{-2} T^{-1} or M T^{-1}
R_h	Heterotrophic respiration	M L^{-2} T^{-1} or M T^{-1}
$R_{maintenance}$	Maintenance respiration	M L^{-2} T^{-1} or M T^{-1}
$R_{overflow}$	Overflow respiration	M L^{-2} T^{-1} or M T^{-1}
T	Biomass turnover	M L^{-2} T^{-1} or M T^{-1}
U	Carbon uptake	M L^{-2} T^{-1} or M T^{-1}

* M: mass, L: length, T: time, -: non-dimensional quantity.

720 **Table 2. Summary of definitions of carbon-use and carbon-storage efficiencies. We are not aware of specific terms used with reference to some of the definitions, as indicated by NA.**

Level of organization	System	Rates/fluxes involved *	Term	Definition	Sources
Organ	Leaf	GPP, NPP, R_a	NA	$\dfrac{\text{Net photosynthesis}}{\text{Gross photosynthesis}}$	This paper
Organism	Heterotrophic microorganisms	U, G, R_h	Yield, apparent yield, C use efficiency, growth efficiency	$\dfrac{\text{Biomass production}}{\text{C uptake}}$	(Payne 1970, van Bodegom 2007)
	Animals	U, G, R_h	Gross growth efficiency	$\dfrac{\text{Biomass production}}{\text{C ingestion}}$	(Sterner and Elser 2002, Doi et al. 2010)
	Plants	U, G, R_a	C use efficiency	$\dfrac{\text{Biomass production}}{\text{Gross photosynthesis}}$	(Cannell and Thornley 2000)
Community	Terrestrial microorganisms	U, G, R_h	C use efficiency	$\dfrac{\text{Biomass production}}{\text{C uptake}}$	(Manzoni et al. 2012, Geyer et al. 2016)
	Aquatic bacteria	U, G, R_h	(Gross) growth efficiency	$\dfrac{\text{Biomass production}}{\text{C uptake}}$	(del Giorgio and Cole 1998)
	Plants	GPP, NPP, R_a	Biomass production efficiency	$\dfrac{\text{NPP}}{\text{GPP}}$	(DeLucia et al. 2007)
Ecosystem	Soil	NECB, NPP	C sequestration efficiency	$\dfrac{\text{C accumulation rate}}{\text{C input rate}}$	(Stewart et al. 2007)
	Sediments	NECB, rate of C burial	Organic C burial (or preservation) efficiency	$\dfrac{\text{C accumulation rate}}{\text{C input rate}}$	(Canfield 1994, Alin and Johnson 2007)
	Vegetation and soil	NEP, GPP	C use efficiency	$\dfrac{\text{NEP}}{\text{GPP}}$	(Fernandez-Martinez et al. 2014)
	Oceanic photic zone	NPP, rate of C export	Particle export ratio	$\dfrac{\text{C export}}{\text{NPP}}$	(Ducklow et al., 2001; Dunne et al., 2005)
	Food webs (producers, consumers, predators)	U, G, R_h	C transfer efficiency, food chain efficiency	$\dfrac{\text{Net biomass product.}}{\text{GPP}}$	(Lindeman 1942, Sterner and Elser 2002)
	Watersheds (vegetation, soil, water bodies)	NECB, GPP	NA	$\dfrac{\text{NECB}}{\text{GPP}}$	This paper

* Symbols and acronyms refer to fluxes depicted in Fig. 1 and 2.

Table 3. Processes associated to the terms of Eq. (6) and (10) at different levels or organization (indicated as subscripts).

System	U	G	R	T	EX (and EG)	Main F_{in}, F_{out}
Leaves (CUE_{leaf})	Gross photosynthesis	Net photosynthesis	Dark respiration, photorespiration	Senescence		-
Microorganisms and microbial communities ($CUE_{microbial}$)	Organic C uptake	Net biomass production	Growth, maintenance, overflow respiration	Cell decay, predation	Extracellular polysaccharides and enzymes	-
Animals (CUE_{animal})	Food ingestion	Net biomass production	Growth, maintenance, overflow respiration	Mortality, predation	Mucus and DOC exudation (and egestion)	-
Plants and plant communities (CUE_{plant})	Gross photosynthesis	Net primary productivity	Growth, maintenance	Mortality, senescence, herbivory	Root exudates, C export to symbionts	Biomass loss due to disturbance, gaseous C other than CO_2
Soils (CSE_{soil})	Litterfall and rhizodeposits ($\approx$NPP)	Net soil C balance	Heterotrophic respiration	-	-	Leaching, erosion, throughfall
Sediments ($CSE_{sediment}$)	NPP ($\approx$0 in deep sediments)	Net sediment C balance	Heterotrophic respiration	-	-	Deposition
Ecosystems ($CUE_{ecosystem}$, $CSE_{ecosystem}$)	Gross primary productivity	Net ecosystem productivity	Autotrophic and heterotrophic respiration	-	-	gaseous C other than CO_2 (for CSE: leaching, erosion, deposition)
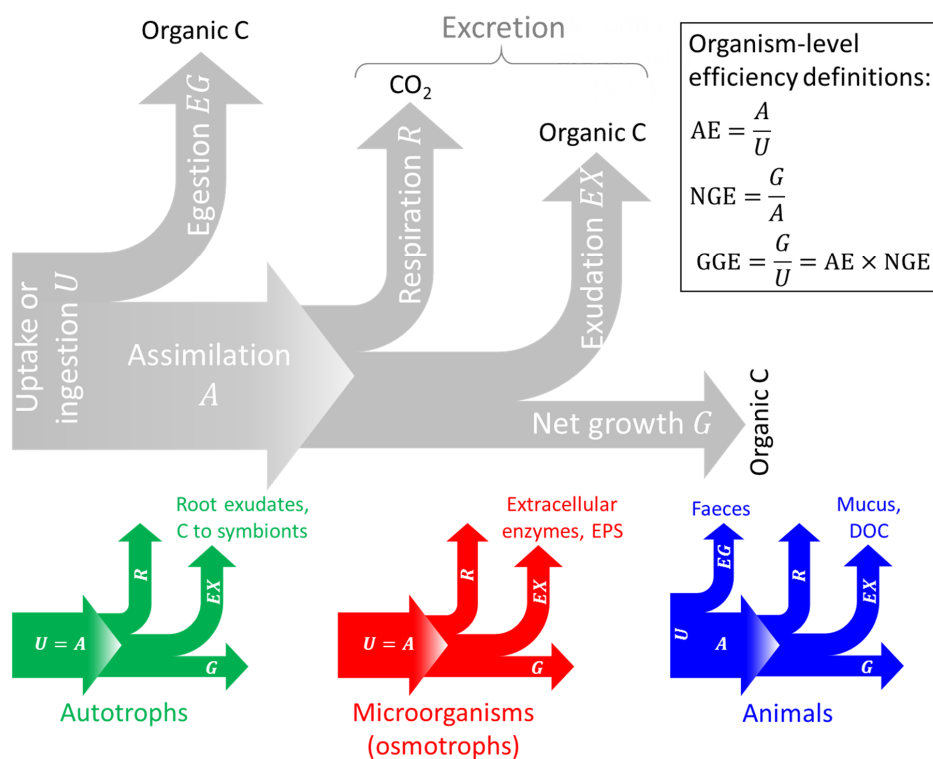
Figure 1. General conceptual summary of C exchanges of individual organisms (or populations). Top: general terminology and C-based efficiency definitions (Sterner and Elser, 2002). Bottom: C exchanges of autotrophs, microorganisms feeding through the cell membranes (osmotrophs), and animals; note that assimilation is equal to uptake (or ingestion) in autotrophs and osmotrophs that lack guts, so that egestion cannot occur. The type of excretion product is also indicated (EPS: extracellular polysaccharides). Colour codes for the different organisms are used also in other figures.

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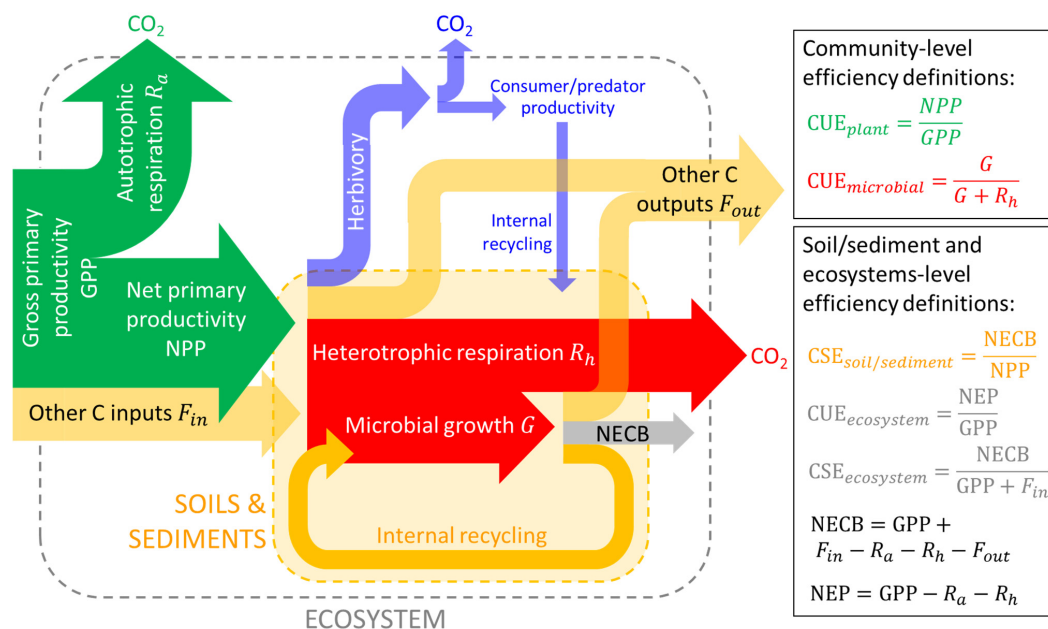

735 **Figure 2. Conceptual scheme of C fluxes in a generic ecosystem, following the terminology by Chapin et al. (2006), but adding the herbivory pathway. The ratio between the flux of C retained in a given sub-system (e.g., vegetation in green, microbial biomass in red, soil and sediments in yellow, whole ecosystem in grey) over the C flux taken up represents the C-use efficiency (CUE) of that sub-system. The net ecosystem C balance is denoted by NECB and the net ecosystem productivity by NEP (not shown). C transport processes and C exchanges in forms other than CO₂ are denoted 'Other**

740 **C inputs/outputs'. A detailed scheme of C exchanges by each sub-system is shown in Fig. S1. Colour codes for the different organisms and sub-systems are used also in other figures.**

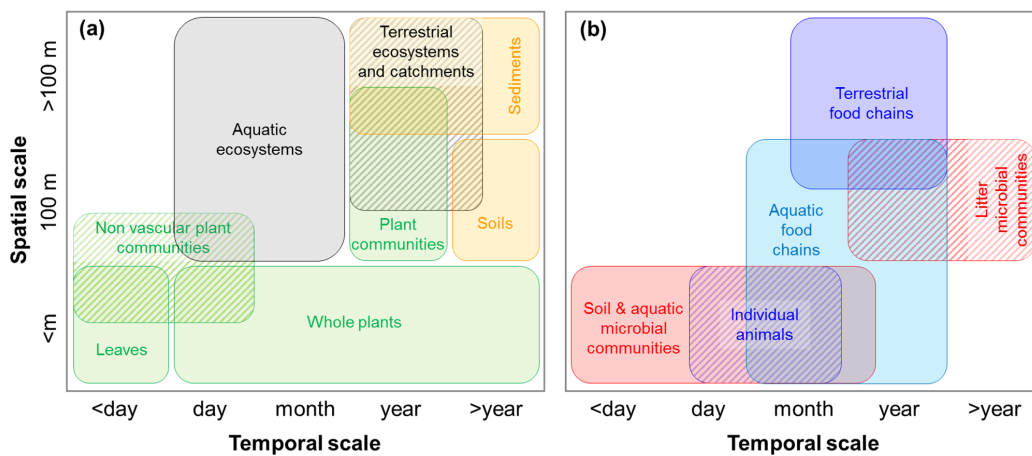



Figure 3. Illustration of typical spatial and temporal scales at which C fluxes are calculated to estimate CUE (or CSE)

745   **in various sub-systems. a) Scales typical of observations on vegetation, whole ecosystems, and soils/sediments; b) scales**

typical of observations on heterotrophic organisms and food chains. Colour codes are as in Fig. 2.

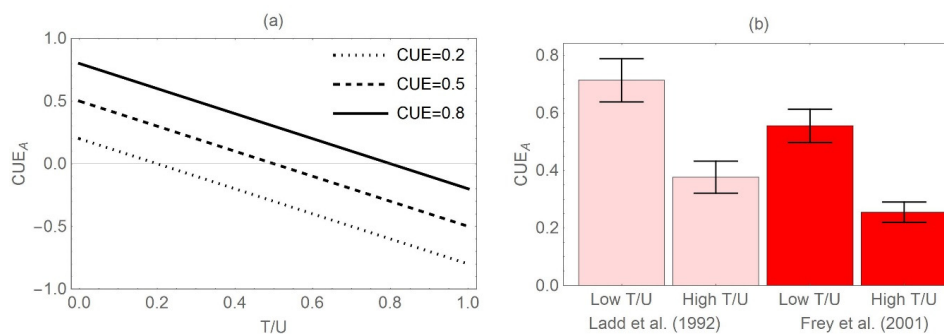



Figure 4. Effect of biomass turnover rate on the apparent C-use efficiency (CUE_A). (a) Theoretical relation between
750   **CUE_A and the ratio of turnover rate over C uptake rate ($\text{CUE}_A = \text{CUE} - T/U$, Eq. (8)), for three values of the actual**
CUE. (b) Two examples of how high turnover rates cause a decrease in CUE_A in empirical studies on soil microbial
communities (Frey et al., 2001; Ladd et al., 1992). Error bars indicate standard errors of the mean.

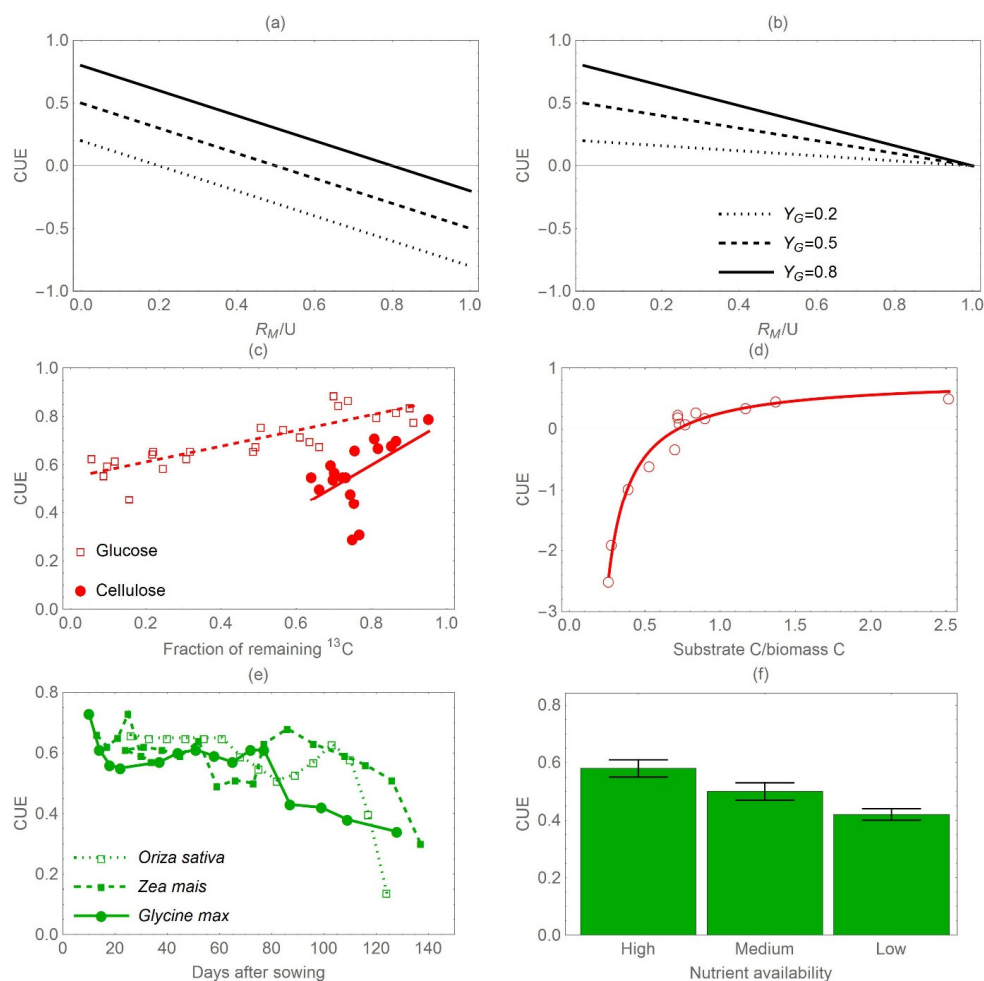



Figure 5. Effect of maintenance respiration ($R_{maintenance}$) on C-use efficiency (CUE). Theoretical relations between

755   **CUE and the ratio of maintenance respiration over C uptake rate in the cases: (a) priority to growth respiration, and**

(b) priority to maintenance respiration, for three values of growth yield (i.e., (C uptake - growth respiration)/C uptake).

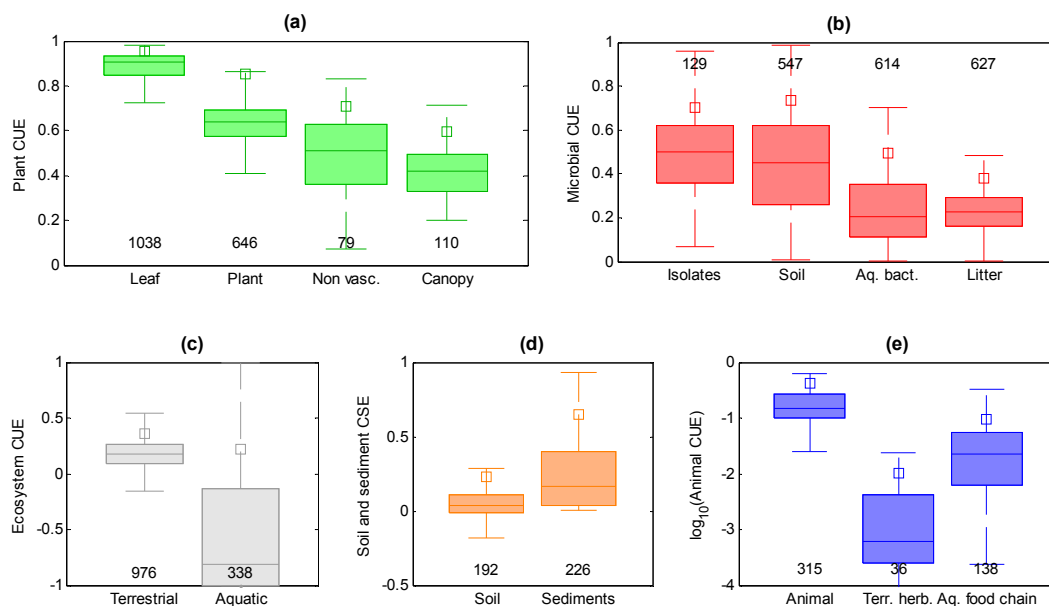
The central panels show decreasing CUE when (c) the C substrate is consumed (moving right to left along the abscissa)

(Öquist et al., 2017) or (d) resource availability (as the ratio of substrate C to biomass C) is low (Collado et al., 2014).

(e) Reduction in CUE through time, as plants end their growth phase and set seeds (Yamaguchi, 1978). (f) Decreasing

760   **forest CUE with decreasing nutrient availability, as C investment to root symbionts increases (Vicca et al., 2012). In (c)**

to (f), CUE decreases as maintenance costs increase relative to growth respiration. Curves in (c) and (d) are least square

linear and hyperbolic regressions drawn to guide the eye; error bars indicate standard errors of the mean.

765 **Figure 6. Patterns in C-use efficiency (CUE) across scales and levels of organization. (a) CUE of leaves, whole plants, non-vascular plant communities, and plant canopies; (b) CUE of microbial isolates, and communities of soil microorganisms, aquatic bacteria, and litter microorganisms; (c) CUE of terrestrial and aquatic ecosystems (note that the y-axis extends to -1, indicating C losses larger than primary productivity); (d) C-storage efficiency (CSE) of soils and sediments (note that the y-axis extends to -0.5); (e) CUE of individual animals, terrestrial herbivore communities,**

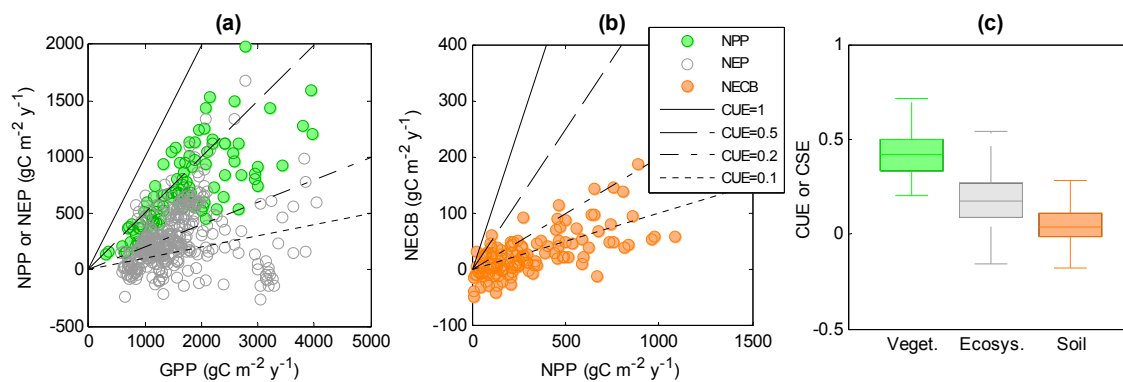
770 **and aquatic food chains, plotted on a log-scale to allow a visual comparison. The box plots display median and quartiles (box), range excluding outliers (whiskers), and the open squares indicate the 90th percentiles; numbers indicate sample sizes; colour codes are as in Fig. 2.**

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Figure 7. Relations between gross primary productivity (GPP) and (a) net primary productivity (NPP) or net ecosystem productivity (NEP), and (b) between NPP and net ecosystem C balance (NECB) in terrestrial systems. In these plots, CUE corresponds to the slopes of lines passing through the origin (four are shown for illustration). (c) Comparison of the CUE or CSE in vegetation, whole ecosystems, and soils (see also Fig. 2). Colour codes are as in Fig. 2.

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