Response to the Editor's Comments

Thanks for the opportunity to submit a revised manuscript following the suggestions of the reviewers. We have already detailed how we planned to revise our manuscript in the responses to the Reviewers' comments posted in the public discussion forum. In this letter, we only describe how the planned changes have been implemented, and leave our arguments for those changes in the open discussion to avoid unnecessary repetitions. Differences between planned and actual changes are mostly editorial, but we also mildly modified the data analysis. Thus, the content of this letter is very similar to that of the previously submitted reviewer response letter.

In addition to the specific responses, we streamlined the text (while also being more careful in distinguishing between CUE and GGE or BPE) and improved most figures (notably adding more complete CUE definitions in Figures 1-2, and changing Figures 5f, 6, and 7, where vegetation CUE values are now based on the dataset by Campioli et al. (2015)). Former Figure S1 was removed as we deemed it unnecessary (the schematic figures in the main text already contained the relevant information). We also modified the way data is presented to make datasets more comparable. Leaf CUE is now estimated at the daily time scale, similar to CUE of nonvascular vegetation (by simply assuming an equal duration of day and night), and to estimate ecosystem CUE, we calculated long-term averages of the C flux data from Luyssaert et al. (2009). This resulted in a smaller, but more self-consistent CUE database compared to the original version. Overall, we feel this revised version is more rigorous and better achieves our goal to provide a consistent definition of CUE across disciplines.

Point-by-point responses are written in italic below.

Anonymous Referee #1

Manzoni et al reviewed and synthesized patterns in carbon use efficiency (CUE) across scales. This is a large effort that can help reconciling previously identified differences in CUE. The authors go into the details of the different definitions that have been used and clarify some of the misunderstandings in the past. I think this could become an important contribution to the field, as differences in definitions and equations for CUE have been mostly ignored and confusion exists on what CUE should reflect. However, I do not fully agree on the presented definitions and think the manuscript still fails to fully resolve discrepancies. The current manuscript does not accurately represented what CUE is, where the term originates from and how it has been used in the past. As the manuscript reads now, I find it a missed opportunity to resolve the confusion that is associated with this topic.

We hope that with this revised version, we come closer to providing a synthesis to resolve inconsistencies in the definitions of CUE.

About the definitions:
From a plant perspective, theory indicates that CUE = NPP/GPP, with NPP = the synthesis of organic compounds = GPP – R. Hence, CUE = 1-R/GPP. (NPP = net primary production; GPP = gross primary production, R = respiration). This corresponds more or less to equation 3 (CUE = 1-outputs/inputs) used by Manzoni et al. However, Manzoni et al consider egestion (EG) and exudation (EX, including symbionts) as part of the outputs, and not as part of NPP. Consequently, the CUE considered here is actually biomass production efficiency (biomass production/inputs = BPE) instead of CUE. Both CUE and BPE are meaningful terms – CUE focusses on the C cycle, while BPE targets the biomass that is produced. In the past, both terms have been rarely distinguished though and they have also not been used consistently.

Correct use can be critical, however, as CUE and BPE may respond differently to environmental changes. For example, an increase in BPE could be associated with un-altered CUE if the partitioning to EX is the sole responsible of the change in BPE (i.e. R unchanged). Such understanding becomes important for example when comparing models with observations. Model evaluation assuming observed BPE = modelled CUE (=1-R/GPP) can lead to serious flaws, as illustrated by the following hypothetical example. Assuming modeled CUE should equal observed BPE, a (hypothetical) decrease of BPE with increasing CO_2 concentration would suggest and increase in R/GPP whereas in reality the decrease in BPE may be solely due to an increase of EX while R/GPP, and hence true CUE, remain unaltered. In this hypothetical example, adjusting the model to reflect observed BPE in modeled CUE would lead to an overestimation of the response of CUE and R to elevated CO_2.

The distinction between CUE and BPE (we use the term 'gross growth efficiency' instead) has been clarified throughout the manuscript, as explained in the following.

The above problem related to the assumption that BPE = CUE is more prominent at some levels (e.g. vegetation) than at others (e.g. bacteria). Hence, differences among levels may in part be due to differences in the definition used. This is somewhat acknowledged by the authors, but it would be much clearer and more accurate if BPE and CUE were clearly distinguished throughout the manuscript and if it was made clear in the figures and tables where BPE is calculated, where CUE is calculated and perhaps also where BPE~CUE.

Following the reviewer's suggestion, the definition of CUE has been modified as:

"We now define CUE at the organism level as the ratio between the rate of production of biomass and products (G+EX), and the rate of C uptake (U),

$$CUE = \frac{G+EX}{U} = \frac{A-R}{U} = 1 - \frac{EG+R}{U}.$$

*As a result, the mass balance equation **Error! Reference source not found.** can be rewritten as,*

$$\frac{dC}{dt} = CUE \times U - EX - T = GGE \times U - T.$$

With this definition, CUE represents the fraction of C taken up that is allocated to biosynthesis (biomass and products that eventually be exuded), but excluding respired and egested C, which do not contribute to biosynthesis. Including exudates such as enzymes and polymeric compounds in the CUE definition may be motivated by the clear fitness advantage these products have for the organism. Moreover, C storage compounds and osmolytes are also regarded as 'biomass', as they would be measured as cellular material.

*Other measures of C conversion efficiency have been proposed (Fig. 1) (Sterner and Elser 2002): i) assimilation efficiency (AE = A/U = assimilation/uptake), ii) net growth efficiency (NGE = G/A = net growth/assimilation), and iii) gross growth efficiency (GGE = G/U = AE × NGE = net growth/uptake, see the last equality on the right hand side of Eq. **Error! Reference source not found.**). The GGE can be regarded as a biomass yield or production efficiency, as it considers respired, egested, and exuded C as lost from the organism (Payne 1970, Manzoni et al. 2012, Campioli et al. 2015), different from CUE, which includes exuded C as a product of the C conversion.*

*The CUE definition in Eq. **Error! Reference source not found.** is consistent with previous work on plant C budgets (Thornley and Cannell 2000), but it differs from definitions often used for soil microorganisms where only biomass synthesis is considered and CUE = GGE (Manzoni et al. 2012, Geyer et al. 2016). It is thus important to emphasize that CUE as defined in Eq. **Error! Reference source not found.** is in general higher than GGE. The difference between GGE and CUE is relevant when EX is large, as in the case of organic C exchanges between roots and plant symbionts (Hobbie 2006, Ekblad et al. 2013), or in anaerobic metabolism (Šantrůčková et al. 2004). In the oceans, 10-30% of microbial production is released as dissolved organic C, but this figure also includes dissolved C from microbial turnover (Benner and Herndl 2011, Jiao et al. 2014). For soil microbial communities, the extent of the extracellular enzyme and polysaccharide synthesis is unknown but presumably small compared to the other rates involved, at least in aerobic soils where CUE≈GGE (Frey et al. 2001, Šantrůčková et al. 2004). Therefore, making the distinction between GGE and CUE is less important in these systems (for further discussions in this context, see Geyer et al. 2016)."*

Further comments in response to the concerns raised by the Reviewer have been added in the Results and Discussion section:

"The effect of increasing exudation rate on CUE varies depending on how such increases are realized. If the increase in EX is fuelled by a correspondingly higher U, CUE also increases; however, if the increase in EX occurs at the expenses of G, such that G+EX is

constant for a given U, CUE will not be affected. In both scenarios, higher EX decreases the net biomass production, and hence lowers GGE. For example, consistent with these expectations, the microbial CUE values of an aerobic soil (where exudation was negligible) and an anaerobic soil (where exudation was ≈2/3 of the net biomass increment), were comparable (respectively 0.73 vs. 0.70), because the sum of exudation and biomass production were similar (Šantrůčková et al. 2004). However, the GGE of the aerobic soil was much higher than in the anaerobic soil (0.72 vs. 0.43)."

A new table has been added in the Supplementary Materials:

Table S3. Comparisons of definitions of C-use efficiencies.

Definitions in this work	Context	Alternative definitions in published literature	Source
$CUE_A = 1-O/I$	Soil microbial communities	Ecosystem-scale efficiency of microbial biomass synthesis and recycling of necromass/exudates (CUE_E)	(Eq. 2 in Geyer et al. 2016)
$GGE = G/U$	Animals and microorganisms	Gross growth efficiency (GGE)	(Sterner and Elser 2002)
	Microbial communities	Carbon use efficiency (CUE)	(Eq. 2 in Manzoni et al. 2012)
	Soil microbial communities	Community-scale efficiency of microbial biomass synthesis (CUE_C)	(Eq. 1 in Geyer et al. 2016)
	Individual plants	Carbon use efficiency (CUE)	(Gifford 1995)
	Plant communities	Biomass production efficiency (BPE)	(Campioli et al. 2015)
$CUE = 1-R/U$	Soil microbial communities	Community-scale efficiency of microbial biomass synthesis when EX≈0 (also denoted as CUE_C)	(Figure 3 in Geyer et al. 2016)
	Plant communities	Carbon use efficiency (CUE = NPP/GPP)	(Cannell and Thornley 2000)

Specific comments: l.26 and l.50: I don't think biomass production/C uptake is the consensus definition of CUE (see above). Intro: I suggest to review the history of the definitions for CUE more elaborately. Where was it first used, what was the exact definition, how have definitions been applied in different fields...

The Introduction was amended as:

"For biological systems (organs, individual organisms, or even entire communities), CUE is defined as the ratio between the amount of C allocated to biosynthesis (new biomass and biological products, including e.g., exudates) and the amount of C taken up. While the term CUE was proposed in the mid-1990s in the context of plant C balances (Gifford 1995), other terms – e.g., 'growth yield' – referring to the efficiency of substrate conversion into biomass had been in use since the early 1900 (Monod 1949). Now, efficiency definitions are proliferating across many disciplines in biology, ecology, and Earth sciences. While some of these definitions are comparable (and all are deceptively simple), subtle differences often

emerge, partly due to conceptual and methodological advances that allow quantification of previously ignored C exchanges. These differences make interpretation of results difficult and complicate cross-disciplinary comparisons.

The main difficulty is to unambiguously define what represents growth, release of extracellular compounds or C storage, and reconcile conceptual definitions with empirical estimates (Clark et al. 2001, Chapin et al. 2006, Geyer et al. 2016)..."

l. 160: clearly define the difference between uptake and assimilation to help the reader in following the different equations

A clarification was added: "where U is the uptake rate, U-EG is the assimilation rate (i.e., A in Fig. 1), and G is the net growth rate."

l.175: define overflow respiration. Ion uptake respiration is not mentioned. Is it considered part of growth respiration? See for example Lambers et al 1983, Physiologia Plantarum, 58: 556-563.

A clarification was added: "Respiration in Eq. **Error! Reference source not found.** *can be further broken down into growth (R_{growth}), maintenance ($R_{maintenance}$), and overflow ($R_{overflow}$) components, the latter including futile cycles and compensation of stoichiometric imbalances that are activated when C cannot be used for growth or maintenance (Russell and Cook 1995, Cannell and Thornley 2000, Thornley and Cannell 2000, van Bodegom 2007).".*

l.200: replace 'reduces' with 'can be simplified to'.
l.222: add 'and to EX' after 'exports to other parts of the plant'.
l.295: I suggest to replace 'lower estimates of CUE' by 'an underestimation of CUE'.
l.444: 'for a given uptake rate' seems more logical than 'for a given respiration rate'.

We have either implemented the suggested changes, or the sentences where the ambiguities were have been heavily modified during re-writing.

I think the authors missed some relevant publications. Cotrufo et al 2013 (Global Change Biology 19, 988-995) discuss the influence of substrate quality on microbial substrate use efficiency (another alternative for CUE), and consequences for soil C storage. This framework deserves at least a mention.

A comment was added citing the suggested paper: "It could be argued that with more efficient organisms, the ecosystem-level CUE would increase, resulting in larger C accumulation (for soil systems, see Cotrufo et al. 2013). There is indeed evidence that microbial communities with higher CUE enhance soil C storage in terrestrial systems (Kallenbach et al. 2016).".

Campioli et al 2015 (Nature Geoscience 8, 843-846) provide an update of Luyssaert et al 2007 and Vicca et al 2012 (both cited in the manuscript), and include also other vegetation types than forests. Data are provided in the supplementary files. I suggest considering including these data, or at least refer to them.

We now refer to the paper by Campioli et al. (2015) and use their dataset in Figures 5, 6, and 7.

Table 2: Cannell and Thornley 2000 actually used the definition CUE = 1- Ra/GPP.

We have moved the citation to Cannell and Thornley (2000) to the correct position in the table, next to DeLucia et al. (2007), and cited here Gifford (1995) instead.

DeLucia et al 2007 used data on biomass production/GPP but termed it NPP/GPP (hence ignoring other NPP components such as exudates and symbionts). This is part of the confusion and I suggest the authors take the opportunity to clarify this.

The Supplementary information was amended as:

"As shown in Eq. (5) in the main text, plant community CUE should be calculated by including both net biomass increments and exudation rates. When only net biomass increments are available, the terms gross growth efficiency (GGE) or biomass production efficiency (BPE) are more accurate (as in Vicca et al. 2012, Campioli et al. 2015). BPE estimates are reported in an extensive global database for forest sites, including direct measurements, indirect estimates (derived from measurements of other C fluxes) and model results (Luyssaert et al. 2007). This dataset has been recently expanded to grasslands and croplands (Campioli et al. 2015) (data used in Fig. 5-7)."

Fig. 2: CUEplant is defined as NPP/GPP, but NPP is undefined. In line with my earlier comments, I suggest to clearly define NPP.

We have now clearly defined NPP in the main text and in the SI.

Figs. 6 and 7: clarify where the data originate from (refer to SI)

We now refer to the SI by adding: "Data sources are described in the Supplementary Information."

Anonymous Referee #2

The manuscript submitted by Manzoni et al. is a review associated to a database analyse around the concept of carbon use efficiency and carbon storage efficiency.

The quality of the manuscript is very high and I particularly appreciated the effort of the authors to gather data from very different sources to have a broad view of the CUE/CSE concept. The writing is excellent and despite the complexity of the question the authors succeed to make a clear and easy to read document. I am convinced that this paper will be provide an important contribution to the literature and since it deals with data coming from plants, soil, ocean, etc. at different spatiotemporal scales it is of broad interest.

I may have few minor comments to try to make the manuscript even more attractive.

Section 3. Can you provide a bit more details on the methods used to collect the data (e.g. keywords used in ISIWEB).

We have added a paragraph in Section 3 "Data collection and analysis":

"To compile the new data collections, we conducted an online search using ISI Web of Science and Google Scholar with keywords including various synonyms of CUE or CSE. We also gathered publications following relevant references in articles and books, aided by the expert knowledge of the authors. Due to the enormous variability in terminology used across disciplines, and the fact that in many cases CUE or CSE were not reported in the papers (but only C exchange rates to calculate them), a systematic search was not feasible. Nevertheless, while not exhaustive, our selection of publications covers a broad range of conditions for each subset of data, enabling detection of general patterns across disciplines and scales."

Section 4.1 You cite two studies as example but some methodological details are missing to fully understand your arguments (what kind of carbon added (litter, glucose...) or how long was the incubation for instance).

Details have been added in the main text to indicate the added compound used (glucose in both cases), and further clarifications have been added in the caption of Figure 4:

"Lower turnover rates were caused by lower mortality in the first 3 days of incubation compared to the day 112 (Ladd et al. 1992), or by lower grazing in the first two days of incubation compared to days 7-8 (Frey et al. 2001). Error bars indicate standard errors of the mean (variability is across three soil types in Ladd et al. (1992) and across replicates and soil types in Frey et al. (2001))."

and in the caption of Figure 5:

"The central panels show decreasing CUE when (c) the C substrate is consumed (moving right to left along the abscissa) during 12 (glucose) and 71 (cellulose) day incubations (Öquist et al. 2017) or (d) resource availability (as the ratio of salicylic acid C to biomass C) is low (Collado et al. 2014)."

I missed some words on the anthropogenic effect on ecosystems CSE. In all the manuscript you compared different types of ecosystems but it may be interesting to compare systems

highly managed like cropland or European forest and grassland with a substantial fraction of the NPP appropriated by humans (see Krausmann et al. (2013) for instance).

This topic is now discussed in Section 4:

" A large fraction of land and of marine systems is managed to extract food and fibre to support a growing human population (Krausmann et al. 2013). Management of ecosystems has two contrasting effects on CSE, depending on the balance of harvest removal, improved production, and organic amendments. On the one hand, extracting harvested products ($F_{out} > 0$) lowers CSE because a lower fraction of GPP remains in the system. For example, assuming a crop harvest index ranging from 25 to 50% of aboveground biomass (e.g., Unkovich et al. 2010) and a 30% allocation to roots, the percentage of NPP harvested and the corresponding reductions in CSE would range from 17 to 33% (Eq. **Error! Reference source not found.***). On the other hand, management may improve CSE by increasing the production efficiency of vegetation (Campioli et al. 2015), or involve addition of organic C to fields ($F_{in} > 0$; e.g., manure or biochar). These C amendments increase CSE for given respiration and harvest rates, not only thanks to their direct effect through F_{in}, but also thanks to indirect effects when soil amendments promote plant productivity. However, this positive effect lessens as the amended organic C is respired and soil organic C reaches saturation levels (Stewart et al. 2007). "*

As a modeller I have a very selfish request (but I guess it may help others). I appreciated the section 4.5 but I guess that the majority of the modellers using CUE concept are aware of the limitations presented here. Maybe one or two paragraphs with some concrete recommendations will be helpful. In particular, I am wondering if CUE or CSE at organisms or ecosystem levels should be considered as emerging properties of a given system and if yes it might become an interesting approach to evaluate model by comparing the CUE/CSE observed at the system level.

We have added the following paragraph to Section 4.5:

"In addition to the correct attribution of changes in CUE to processes or environmental conditions, it remains critical to match the definition of CUE used by empiricists with that implemented in models. Specifically, are the same biosynthesis components (e.g., biomass increment vs. exudate export) accounted for in both empirical efficiency estimates and in the model equations? Are abiotic C exchanges at the ecosystem scale both included in empirical estimates of CSE and described by models? As CUE and CSE represent emerging properties of organisms and ecosystems, they are appealing for model testing, but without a consistent definition, comparisons of model outputs and empirical estimates are not meaningful. "

Anonymous Referee #3

The manuscript is descriptive without a very extensive data analysis. However, the synthesis is new (I've never read about such large comparison of CUE across biological systems and biological scales) and interesting (I particularly like the fundamental Fig. 6). So, I think the manuscript is suited for publication without a data re-analysis.

Even if not explicitly requested, we modified the data analysis to improve comparability among datasets in our database, as explained in Section 3:

"To facilitate comparisons across datasets, instantaneous CUE values estimated for leaves and non-vascular plant communities were converted to daily values by assuming an equal duration of day- and night-time, and that respiration rates were the same throughout the whole day. Moreover, plant community and ecosystem C fluxes (Luyssaert et al. 2007, Campioli et al. 2015) were averaged first when estimates from different approaches were reported for a given site and year, and second across years to provide long-term mean fluxes."

However, there are key points that need to be improved (do not underestimate them, even are just text improvements). The Theory (paragraph 2) and definitions are fundamental in this paper, yet are not fully clear.

*for all biological systems, you use the term CUE. However, as well reported in Table 2, for some systems other terms are used. Furthermore, CUE is associated to a specific variable/system (plant and community CUE=NPP/GPP). It would have been much less confusing (and more relevant) if you were proposing an overarching (new) efficiency term, and not 'impose' the one used for some systems to all cases.

We have revised the paragraph on the definition of CUE definition as (see also responses to Reviewer 1):

"We now define CUE at the organism level as the ratio between the rate of production of biomass and products (G+EX), and the rate of C uptake (U),

$$CUE = \frac{G+EX}{U} = \frac{A-R}{U} = 1 - \frac{EG+R}{U}.$$

As a result, the mass balance equation **Error! Reference source not found.** *can be rewritten as,*

$$\frac{dC}{dt} = CUE \times U - EX - T = GGE \times U - T.$$

With this definition, CUE represents the fraction of C taken up that is allocated to biosynthesis (biomass and products that eventually be exuded), but excluding respired and egested C, which do not contribute to biosynthesis. Including exudates such as enzymes and polymeric compounds in the CUE definition may be motivated by the clear fitness advantage these products have for the organism. Moreover, C storage compounds and osmolytes are also regarded as 'biomass', as they would be measured as cellular material."

*your attempt of generalization (paragraph 2) is not always easy to follow because each domain (plant, micro-organisms, ecosystems etc.) has his own specific definitions and

terminology. It would be easier if you, before generalize (so before paragraph 2.1), describe the specific ways CUE is calculated for each of the five 'scales' you synthesize in Fig 6, thus an extension of Table 2. And then, when you generalize, make several examples. For instance, what is 'Output' (Eq. 1) for the five scales?

We implemented the suggestion to clarify what 'input' and 'output' represent for the various systems we considered. Specifically, we revised Table 3 by restructuring the columns and highlighting which components of the C cycle are inputs or outputs for each system and scale. The table heading has been changed as follows:

System	Inputs			Outputs			
	U	G	F_{in}	R	T	EX (and EG)	F_{out}

*There are the definitions used in the field-specific literature (Table 2) and you add other definitions: CUEapparent, AE, NGE, GGE, CUE ecosystem (extremely confusing: NPP/GPP or NEP/GPP?). Make some choices (can the definitions be reduced?) and clarify.

We have not made specific changes in response to this comment (see our rationale in the response to reviewers' comments in the public discussion).

*For some cases, you mention the possibility of negative CUE, but for plant (CUE=NPP/GPP) it would not be possible because NPP>0 or =0). Similarly, turnover has a meaning for microbes and another for plants (e.g. in forests, turnover refers to the annual leaves, branch or root turnover and it is added in NPP, Clark et al 2001 Ecological Application 11(2), pp. 356–370).

We have not made specific changes in response to this comment (see our rationale in the response to reviewers' comments in the public discussion).

Other remarks
*Your main key syntheses were (from abstract): (i) CUE increases with improving growing conditions, (ii) CUE decrease due to turnover, (iii) CUE decreases with increasing biological and ecological organization. Write them also in Conclusions (instead of generic sentences from L497 to L505) with the key reasons/explanations.

The Conclusions have been rewritten as:

*"We have synthesized definitions of and explored variations in the efficiency of C use by organisms, communities 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 terminological and interpretation issues. In particular, the same term CUE (but also other synonyms) is often used at organism-to-community scales to indicate actual C-use efficiency (Eq. **Error! Reference source not found.**), apparent C-use efficiency (related but not equal to CUE, Eq. **Error! Reference source not found.**), and gross growth efficiency. This mixed use may cause misinterpretations, as it is not clear whether turnover and biological products are included in the CUE calculations. Similarly, at the ecosystem scale the term CUE is used without specifying whether abiotic and anthropogenic fluxes are accounted for. For improved clarity, we suggest to always define how*

CUE is estimated with particular attention to C exchanges other than biomass increments and respiration.

  Our synthesis shows that turnover deflates 'apparent' CUE estimates, but not 'actual' CUE calculated as biosynthesis over C uptake ratio. Improving growing conditions generally increases CUE and CSE because it promotes growth processes over C loss processes. Finally, CUE tends to decrease with the level of ecological organization – e.g., from rapidly growing individual organisms to natural communities and ecosystems – as less efficient individuals are considered in communities and more heterotrophic components are sequentially added to the system. Because CUE and CSE are outcomes of a wide spectrum of processes, they are expected to be flexible and to respond to both biological (e.g., trends in growth vs. respiration) and physical controls (e.g., C transport and environmental conditions). As such – and provided that empirical and model definitions of these efficiencies are consistent – 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."

*L320-321: as in plants CUE= NPP/GPP and seed production is accounted in NPP, I do not understand your point

We added a clarification: "Similarly, crops maintain a high CUE until they stop growing vegetative tissues, which senescence while resources are translocated to seeds"

*L503 can be moved above where you discuss applicability of CUE values.

This sentence has been moved as suggested.

*You do not make reference to Campioli et al 2015 Nat Geo. However, that synthesis can be useful, not only for the additional dataset on CUE (that they consider BPE there) but for comparison of ecosystems of different complexity (e.g. natural grassland vs. cropland monoculture). Also there are various suggestions for practical use of CUE/BPE in that paper.

Thanks for pointing out to this publication, which is now cited and used extensively in our manuscript.

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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 biosynthesis. In soils and sediments, C storage also 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 watersheds, and soils and sediments using a common mathematical framework. Second, we identify general CUE patterns; e.g., the actual CUE increases with improving growth conditions, and apparent CUE decreases with increasing turnover. We then synthesize >5000 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 and 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 biomass and

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biological products 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; Hessen et al., 2004; Jiao et al., 2014; Sterner and Elser, 2002). 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 biosynthesis (new biomass and biological products, including e.g., exudates) and the amount of C taken up. While the term CUE was proposed in the mid-1990s in the context of plant C balances (Gifford, 1995), other terms – e.g., 'growth yield' – referring to the efficiency of substrate conversion into biomass had been in use since the early 1900 (Monod, 1949). Now, efficiency definitions are proliferating across many disciplines in biology, ecology, and Earth sciences. While some of these definitions are comparable (and all are deceptively simple), subtle differences often emerge, partly due to conceptual and methodological advances that allow quantification of previously ignored C exchanges. These differences make interpretation of results difficult and complicate cross-disciplinary comparisons.

The main difficulty is to unambiguously define what represents growth, release of extracellular compounds or C storage, and reconcile conceptual definitions with empirical estimates (Geyer et al., 2016; Chapin et al., 2006; Clark et al., 2001). In fact, CUE is a property of the biological system considered under the specific conditions it experiences, and synthetizes various biological processes occurring across a range of spatial and temporal scales in a single variable (Geyer et al., 2016). Because the proportion of growth vs. maintenance respiration, the growth rate, the synthesis and release of products, and the availability of C all vary in time in any organism, CUE is also expected to change. Changes in environmental conditions that favour growth over respiration will shift the balance of C allocation towards biosynthesis (or C storage at the ecosystem level), 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 populations, 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; Geyer et al., 2016). 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.,

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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 transport processes. The more C is removed via, e.g., leaching and lateral transfer (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 also depends 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; e.g., in the uppermost organic layers of forest soils or in peatlands. Moreover, as C is recycled in the soil or sediment system and progressively more C is lost, C accumulation becomes more dependent on physico-chemical protection mechanisms that reduce accessibility of C to decomposers and abiotic 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 important for correct partitioning of C in biogeochemical models, in which these efficiencies are sometimes assumed constant (e.g., microbial CUE), and in other cases 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.

With this aim in mind, we synthesize the numerous definitions of C-use and C-storage efficiencies 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 physico-chemical processes that lead to stabilisation or incomplete turnover of organic matter become relevant to evaluate C retention at the whole-ecosystem level. While previous syntheses have investigated drivers of CUE in specific systems (Canfield, 1994; del Giorgio and Cole, 1998; DeLucia et al., 2007; Manzoni et al., 2017; Sinsabaugh et al., 2015; Sterner and Elser, 2002), we focus 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 observed trends in relation to our understanding of the C cycle, for informing ecosystem model development, and for overcoming disciplinary boundaries that have led to numerous conceptually similar CUE 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 communities), in which C is actually 'used' for functions related to the fitness of organisms, either as individuals

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165 or in communities. 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 and all quantities are expressed in carbon units. Table 2 summarizes the different definitions of CUE proposed in the literature, and Table 3 relates C

170 exchanges rates and fluxes used in the theory section to processes specific to the system under consideration.

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,

175 and are defined differently for organisms and ecosystems, as discussed in the following. In this general equation, 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) – the ratio of C remaining in the system (i.e., $\frac{dC}{dt}$) over C added to the system (I). The term CUE_A is used for convenience, noting that CSE_A should be used for systems involving abiotic C exchanges. This is an 'apparent' efficiency because it is calculated solely from C input and change in storage,

180 without any consideration of the underlying processes that determine the C outputs. As will become clear, this pragmatic definition is insufficient for CUE to have a biological meaning. Based on this definition, Eq. (1) can be recast as

$$\frac{dC}{dt} = \text{CUE}_A \times I, \tag{2}$$

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

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

185 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 in storage and input rate. For systems in which inputs are larger than outputs, $0 < \text{CUE}_A < 1$. In contrast, when outputs are larger than inputs, the system loses mass and $\text{CUE}_A < 0$. For biological systems where C represents the biomass of the organism, CUE_A represents the fraction of C uptake contributing to a biomass increase. Simialr

190 considerations hold for whole ecosystems, and CSE_A is accordingly defined as 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 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

195 mechanistic insight into the processes leading to the allocation of C to storage or output rates. However, Eq. (3) is used to estimate apparent CUE in many practical applications where input, change in storage and/or output are measured – including the estimation of CUE for biological systems. If the observational setup is such that changes

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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 the CUE of that organism. However, in general, a more accurate description of the organism C balance is required to define a biologically meaningful CUE, leading to numerous definitions of CUE (Table 2).

Let us now focus on C compartments representing the biomass of an individual organism or of a community. Here, 'organism' indicates any living entity, ranging from unicellular to multicellular, and including both autotrophs and 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 Table 3, specific processes for each type of organism are matched to the general C balance terms used below. In this context, the input I represents C uptake or ingestion (U), and the output O represents the sum of egestion (EG), respiration (R), exudation (EX), and turnover (T) (Sterner and Elser, 2002); i.e., the output rate is expressed as $O = EG + R + EX + T$ (Fig. 1). Distinguishing among these processes is motivated by the different time scales for respiration (seconds to hours) and turnover (minutes to years) processes. 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 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; Ekblad et al., 2013) 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),

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

where U is the uptake rate, U-EG is the assimilation rate (i.e., A in Fig. 1), and G is the net growth rate. We now define CUE at the organism level as the ratio between the rate of production of biomass and products $(G+EX)$, and the rate of C uptake (U).

$$CUE = \frac{G+EX}{U} = \frac{A-R}{U} = 1 - \frac{EG+R}{U}. \tag{5}$$

As a result, the mass balance equation (4) can be rewritten as,

$$\frac{dC}{dt} = CUE \times U - EX - T = GGE \times U - T. \tag{6}$$

With this definition, CUE represents the fraction of C taken up that is allocated to biosynthesis (biomass and products that eventually be exuded), but excluding respired and egested C, which do not contribute to biosynthesis. Including exudates such as enzymes and polymeric compounds in the CUE definition may be motivated by the clear fitness advantage these products have for the organism. Moreover, C storage compounds and osmolytes are also regarded as 'biomass', as they would be measured as cellular material.

Other measures of C conversion efficiency have been proposed (Fig. 1) (Sterner and Elser, 2002): i) assimilation efficiency (AE = A/U = assimilation/uptake), ii) net growth efficiency (NGE = G/A = net growth/assimilation), and iii) gross growth efficiency (GGE = G/U = AE × NGE = net growth/uptake, see the last equality on the right hand side of Eq. (6)). The GGE can be regarded as a biomass yield or production

efficiency, as it considers respired, egested, and exuded C as lost from the organism (Payne, 1970; Manzoni et al., 2012; Campioli et al., 2015), different from CUE, which includes exuded C as a product of the C conversion.

The CUE definition in Eq. (5) is consistent with previous work on plant C budgets (Thornley and Cannell, 2000), but it differs from definitions often used for soil microorganisms where only biomass synthesis is considered and CUE = GGE (Manzoni et al., 2012; Geyer et al., 2016) (Table S3). It is thus important to emphasize that CUE as defined in Eq. (5) is in general higher than GGE, because $CUE = GGE + EX/U$. The difference between GGE and CUE is relevant when EX is large, as in the case of organic C exchanges between roots and plant symbionts (Hobbie, 2006; Ekblad et al., 2013), or in anaerobic metabolism (Šantrůčková et al., 2004). In the oceans, 10-30% of microbial production is released as dissolved organic C, but this figure also includes dissolved C from microbial turnover (Benner and Herndl, 2011; Jiao et al., 2014). For soil microbial communities, the extent of the extracellular enzyme and polysaccharide synthesis is unknown but presumably small compared to the other rates involved, at least in aerobic soils where CUE≈GGE (Frey et al., 2001; Šantrůčková et al., 2004). Therefore, making the distinction between GGE and CUE is less important in these systems (for further discussions in this context, see Geyer et al., 2016).

Respiration in Eq. (5) can be further broken down into growth (R_{growth}), maintenance ($R_{maintenance}$), and overflow ($R_{overflow}$) components, the latter including futile cycles and compensation of stoichiometric imbalances that are 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,

$$CUE = 1 - \frac{R_{growth} + R_{maintenance} + R_{overflow} + EG}{U} \quad (7)$$

which demonstrates that any increase in the maintenance and overflow respiration rates relative to growth respiration due to starvation or environmental stresses decreases CUE (Sect. 4.1).

Finally, combining Eq. (2) and (6) provides the relation between CUE_A, CUE, and C losses via exudation and turnover,

$$CUE_A = CUE - \frac{EX + T}{U}. \quad (8)$$

Based on this equation, higher turnover or exudation rate reduce CUE_A, but not CUE (Eq. (5)).

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 turnover is incomplete), for which fitness cannot be defined. Examples of such coupled biotic-abiotic systems are whole ecosystems (terrestrial and 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),

$$\frac{dC}{dt} = U + F_{in} - R - F_{out} = NECB. \quad (9)$$

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In Eq. (9), U and R represent respectively the C uptake and respiration rates by the biotic components of the system when considering an entire ecosystem (as in Eq. (4)), whereas U refers to litterfall and C deposition when considering soils and sediments, respectively (Table 3). The F_{in} and F_{out} are C inputs and outputs occurring via abiotic exchanges of organic and inorganic C in natural ecosystems, but also account for anthropogenic inputs (e.g., manure) and outputs (e.g., harvested products) in managed ecosystems. With reference to ecosystems, the C balance of Eq. (9) can also be expressed in terms of the net ecosystem C balance, NECB (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,

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

In a purely abiotic system ($U = R = 0$), Eq. (10) can be simplified to $\text{CSE} = 1 - F_{out}/F_{in}$. In contrast, when the abiotic C rates are negligible ($F_{in} \approx F_{out} \approx 0$), Eq. (10) is simplified to $\text{CSE} = 1 - R/U$ – i.e., the C-use efficiency of the biological components in the system (Eq. (5), with $EG=0$). Based on Eq. (10), CSE>0 when an ecosystem is storing C (e.g., systems with long-term accumulation of C in undecomposed necromass, mineral-associated pools, or sediments). As for Eq. (5), the meaning of the C exchange rates in Eq. (10) depend on the system under consideration – e.g., U=GPP for entire ecosystems, but U=rate of C input to soils when calculating soil CSE (Table 3).

Substituting the definition of CUE for the biological components into Eq. (10) and assuming dominant biological C losses via respiration, an expression linking the system CSE and the biological CUE is found as,

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

This relation 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.

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

Equations (5) and (10) provide general definitions of C-use and C-storage efficiencies, for biological and coupled biotic-abiotic systems, respectively (Table 3). 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, egestion, 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 to actually measure 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 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 and as exudates. Other challenges arise when separating autotrophic and heterotrophic contributions to a single measured respiratory CO_2 flux. Common approaches for measuring C exchange rates relevant for CUE

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and CSE calculations are presented and discussed in the Supplementary Information and the wide range of spatial-temporal scales involved in illustrated in Fig. 3. In our data collection, we compared systems ranging from individual organism and communities, to soils and sediments, food webs, and whole ecosystems and watersheds

415 (Tables 2 and 3).

3 Data collection and analysis

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

420 of heterotrophic organisms (McNaughton et al., 1989; Manzoni et al., 2017), leaves (Atkin et al., 2015), plant communities (Campioli et al., 2015), 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 data collections are developed for CUE of microbial isolates, individual plants, non-vascular vegetation, food chains, soils, and watersheds. The whole database encompasses 5309 CUE estimates.

425 To compile the new data collections, we conducted an online search using ISI Web of Science and Google Scholar with keywords including various synonyms of CUE or CSE. We also gathered publications following relevant references in articles and books, aided by the expert knowledge of the authors. Due to the enormous variability in terminology used across disciplines, and the fact that in many cases CUE or CSE were not reported in the papers (but only C exchange rates to calculate them), a systematic search was not feasible.

430 Nevertheless, while not exhaustive, our selection of publications covers a broad range of conditions for each subset of data, enabling detection of general patterns across disciplines and scales.

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

435 comparisons across datasets, instantaneous CUE values estimated for leaves and non-vascular plant communities were converted to daily values by assuming an equal duration of day- and night-time, and that respiration rates were the same throughout the whole day. Moreover, plant community and ecosystem C fluxes (Campioli et al., 2015; Luyssaert et al., 2007) were averaged first when estimates from different approaches were reported for a given site and year, and second across years to provide long-term mean fluxes. The large majority of data sets

440 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 required the conversion of energy-based to C-based fluxes to calculate CUE (McNaughton et al., 1989). Energy flux data [kJ/m^2/y] were first converted to dry weights using animal and ecosystem-specific plant-community heat of

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

We aim to illustrate the range of variation in CUE across spatial and temporal scales, and levels of biological and ecological organization, but 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. Further, a

450 comparison of CUE estimates across these diverse data sources is also challenging because of the contrasting

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spatial and temporal scales at which measurements were conducted (Fig. 3). As such, and given our aim, we have not attempted to bring individual CUE estimates to a comparable scale. For individual plants and microbial communities, CUE estimation approaches vary, and in some cases GGE was reported. Considering the lack of information on the relevance of exudation rates, for these organisms we grouped published efficiencies under the label CUE. For plant communities in which biomass increments were measured, we use the term GGE (equivalent to biomass production efficiency, as in Campioli et al., 2015).

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) long-term average CUE of plant communities and ecosystems, and CSE of soils (plot-to-field spatial scale and annual-to-decadal 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, with the same approach we test 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 examples on how measured CUE can be driven by 'true' biological factors that affect C partitioning in organisms, but how apparent CUE can 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 CUE 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 and exudation can be neglected, this 'apparent' CUE is a good approximation of the actual CUE (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 glucose

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initially added to the soil is taken up by microorganisms with a certain actual CUE, but as the incubation progresses, the ^{14}C remaining in the microbial biomass decreases partly due to cell turnover. As a result, CUE_A at the beginning of the incubation was 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 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 (glucose) and respiration, estimates were insensitive to grazing pressure (Frey et al., 2001). Similarly decreasing CUE_A has been found in aquatic bacteria subjected 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 underestimation of CUE, when using Eq. (3).

Figure 5 illustrates how the relative importance of maintenance costs (respiration and exudation) as compared to growth respiration alters CUE or GGE. 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 maintenance costs and CUE can become negative, because maintenance can cause a net biomass loss (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 available for growth respiration. In this case, CUE can at the lowest 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. 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. 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.

The effect of increasing exudation rate on CUE varies depending on how such increases are realized. If the increase in EX is fuelled by a correspondingly higher U, CUE also increases; however, if the increase in EX occurs at the expenses of G, such that $G+EX$ is constant for a given U, CUE will not be affected. In both scenarios, higher EX decreases the net biomass production, and hence lowers GGE. For example, consistent with these expectations, the microbial CUE values of an aerobic soil (where exudation was negligible) and an anaerobic soil (where exudation was ≈2/3 of the net biomass increment), were comparable (respectively 0.73 vs. 0.70), because the sum of exudation and biomass production were similar (Šantrůčková et al., 2004). However, the GGE of the aerobic soil was much higher than in the anaerobic soil (0.72 vs. 0.43).

For example, the CUE and GGE of microbial communities tend to be low just after addition of a labile C substrate (a 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 catabolic conversion of biomass to cover maintenance respiration, CUE<0 (Fig. 5d). Similarly, crops maintain a high CUE until they stop growing vegetative tissues, which senescence while resources are translocated to seeds (Fig. 5e). In forests, GGE (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 more likely to higher C investment in plant symbionts (Campioli et al., 2015; Baskaran et al., 2017). Because the effects of higher maintenance respiration or exudation rate have the same direction – both decreasing GGE – we can expect that along resource or environmental gradients characterized by increasing maintenance costs (including exudation), GGE will decrease. Along the same gradients, CUE would decrease only if maintenance costs increase, while it would be unaffected by changes in exudation rates alone.

A somewhat similar argument has been proposed to explain increases in GGE with increasing nutrient-to-C ratios of the resources used by heterotrophic organisms (Manzoni et al., 2017, where the term CUE was used under the implicit assumption CUE≈GGE). High nutrient availability with respect to C allows growth of the nutrient-rich cells typical of heterotrophs in C limited conditions. 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 growth, leading to reduced GGE under conditions of nutrient shortage (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 entire 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≈0.8, Fig. 6a), as might be expected for the organ responsible for entry of C into the biosphere. While leaves only have to support their own limited metabolic needs, whole plants require energy to maintain a range of additional functions, including nutrient uptake and use, regulation of ion balances and phloem transport (Cannell and Thornley, 2000; Thornley and Cannell, 2000). Thus, 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, 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). 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

630 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*.

635 Food webs include interacting organisms that exchange C among them and with the environment. Each 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. The 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 (Fig. 6e). Moreover, antagonistic interactions in a food web may increase metabolic costs, also

640 lowering CUE (Toljander et al., 2006). Similar to the organism-level responses to resource availability, also C transfer efficiencies tend to be higher in resource-rich environments. For example, the fish-to-phytoplankton production ratio is higher under 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 C:N litter, despite no observable difference in C input (Frouz et al., 2013a). In the latter example, it is important to emphasize the

645 role of soil fauna in mediating this response to nutrient availability – the presence of macro-fauna facilitates the transport of C towards sites where it can be stabilized (via bioturbation).

Like moving from simple towards more complex organisms or from single individuals to interacting organisms in food webs, consideration of whole ecosystems also results in lower C retention capacity compared to individual organisms and communities. Aggregation of processes results in a lower CUE for a given GPP, in

650 particular when adding more heterotrophic components (Fig. 2). In fact, 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 ≈ 0.4) than that for ecosystems (CUE≈0.2). Ecosystem CUE is expected to be lower than the soil C storage efficiency, because ecosystem CUE

655 is the product of soil CSE (=NECB/NPP, with NPP: net primary productivity) and vegetation CUE (=NPP/GPP, with GPP: gross primary productivity; Supplementary Materials Section 1.6). This is not the case in the data presented in Fig. 7, where the median soil CSE is significantly lower than the median ecosystem CUE. This unexpected result could be explained by the fact that in agricultural systems such as those we used to estimate soil CSE, soil disturbance strongly reduces C accumulation compared to a natural system.

660 We can also ask how the CUE of individual ecosystem components affects the overall ecosystem CUE. It could be argued that with more efficient organisms, the ecosystem-level CUE would increase, resulting in larger C accumulation (for soil systems, see Cotrufo et al., 2013). There is indeed evidence that microbial communities with higher CUE enhance soil C storage in terrestrial systems (Kallenbach et al., 2016). However, decomposers alter the kinetics of decomposition via extracellular enzymes that are thought to be produced in proportion to the

665 living biomass (Schimel and Weintraub, 2003). As a result of these feedbacks, it is possible that lower (rather than higher) decomposer CUE increases ecosystem CUE and thus C storage potential, as indicated by empirical studies in boreal forests (Kyaschenko et al., 2017) and modelling results (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),

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the CSE of lacustrine and marine sediments is significantly higher than that of soils (Fig. 6d). The first pattern is explained by allochthonous C contributions to respiration (Sect. 4.3). This explanation should hold also considering that aquatic ecosystem CUE are calculated from daily fluxes, whereas terrestrial ecosystem CUE are calculated from long-term (inter-annual) mean fluxes. In contrast, the higher CSE of sediments than of soils can be explained by the often high sedimentation rate (Calvert et al., 1992) and the relatively short exposure time to oxygen after burial of organic C (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; $p<0.05$). 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 higher levels of biological or ecological organization generally imply 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 opposed to primary producers 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 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 under field conditions, where also inactive or slowly growing individuals are included results in lower population- or community-level CUE. In the case of plants, CUE of individuals is on average around 0.6, whereas in plant communities GGE≈0.4 (Fig. 6a). Part of this difference might be attributed to exudation rates that cause CUE>GGE, but other interpretations are also possible. 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, 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 CUE of soil microbial communities could be due to generally higher resource availability in soils than in aquatic environments, or to amendment of soils with labile compounds that stimulate microbial activity and mask the contribution of slow-growing organisms (Sinsabaugh et al., 2013).

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

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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 remain high while growth stagnates. As mentioned in Sect. 4.2, this could explain why long-term CUE of litter microorganisms is lower than microbial CUE measured over short periods in other systems (Fig. 6b).

4.4 Interpreting C-use and C-storage efficiencies in systems with abiotic and anthropogenic 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 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. (10)). 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 negative. Despite inland aquatic 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)), as well as accumulation of dissolved inorganic C.

Physical removal of C also alters the estimated CSE. Because physical removal reduces the C that can be stored for a given uptake rate, CSE decreases with increasing abiotic losses of C (F_{out}). When these losses of C are considered in addition to respiration, 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 average ecosystem CUE=0.137, whereas including abiotic losses leads to CSE=0.104 – i.e., a >30% reduction in 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).

A large fraction of land and of marine systems is managed to extract food and fibre to support a growing human population (Krausmann et al., 2013). Management of ecosystems has two contrasting effects on CSE, depending on the balance of harvest removal, improved production, and organic amendments. On the one hand, extracting harvested products ($F_{out} > 0$) lowers CSE because a lower fraction of GPP remains in the system. For example, assuming a crop harvest index ranging from 25 to 50% of aboveground biomass (e.g., Unkovich et al., 2010) and a 30% allocation to roots, the percentage of NPP harvested and the corresponding reductions in CSE would range from 17 to 33% (Eq. (10)). On the other hand, management may improve CSE by increasing the production efficiency of vegetation (Campioli et al., 2015), or involve addition of organic C to fields ($F_{in} > 0$; e.g., manure or biochar). These C amendments increase CSE for given respiration and harvest rates, not only thanks to their direct effect through F_{in}, but also thanks to indirect effects when soil amendments promote plant productivity. However, this positive effect lessens as the amended organic C is respired and soil organic C reaches saturation levels (Stewart et al., 2007).

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4.5 Do we need C-use efficiency estimates?

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). In fact, 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. On the other hand, full process understanding requires identification of these drivers and in 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 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 (i.e., 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).

Moreover, non-dimensional numbers – such as CUE and CSE – emerge as key drivers of system dynamics (Vogel, 1998; Buckingham, 1914; Feng et al.). 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 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 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). Empirically established patterns of variation in CUE thus help identification of systems and conditions under which CUE is indeed stable or, in contrast, when additional processes 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 under natural conditions. Apart from possible scale mismatches between empirical estimates of CUE and model interpretation, models that assume a stationary set of metabolic responses could underestimate C retention. This is the case when CUE acclimates and buffers the 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-

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845 successional species – these models might underestimate potential feedbacks between the biosphere and global climate.

In addition to the correct attribution of changes in CUE to processes or environmental conditions, it
remains critical to match the definition of CUE used by empiricists with that implemented in models. Specifically,
are the same biosynthesis components (e.g., biomass increment vs. exudate export) accounted for in both empirical
850 efficiency estimates and in the model equations? Are abiotic C exchanges at the ecosystem scale both included in
empirical estimates of CSE and described by models? As CUE and CSE represent emerging properties of
organisms and ecosystems, they are appealing for model testing, but without a consistent definition, comparisons
of model outputs and empirical estimates are not meaningful.

5 Conclusions

855 We have synthesized definitions of and explored variations in the efficiency of C use by organisms, communities
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 terminological and
interpretation issues. In particular, the same term CUE (but also other synonyms) is often used at organism-to-
community scales to indicate actual C-use efficiency (Eq. (5)), apparent C-use efficiency (related but not equal to
860 CUE, Eq. (8)), and gross growth efficiency. This mixed use may cause misinterpretations, as it is not clear whether
turnover and biological products are included in the CUE calculations. Similarly, at the ecosystem scale the term
CUE is used without specifying whether abiotic and anthropogenic fluxes are accounted for. For improved clarity,
we suggest to always define how CUE is estimated with particular attention to C exchanges other than biomass
increments and respiration.

865 Our synthesis shows that turnover deflates 'apparent' CUE estimates, but not 'actual' CUE calculated as
biosynthesis over C uptake ratio. Improving growing conditions generally increases CUE and CSE because it
promotes growth processes over C loss processes. Finally, CUE tends to decrease with the level of ecological
organization – e.g., from rapidly growing individual organisms to natural communities and ecosystems – as less
efficient individuals are considered in communities and more heterotrophic components are sequentially added to
870 the system. Because CUE and CSE are outcomes of a wide spectrum of processes, they are expected to be flexible
and to respond to both biological (e.g., trends in growth vs. respiration) and physical controls (e.g., C transport
and environmental conditions). As such – and provided that empirical and model definitions of these efficiencies
are consistent – 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.

875 **Data availability**

The datasets supporting the results that are not already published will be archived in the open-access database of
the Bolin Centre for Climate Research (https://bolin.su.se/data/Manzoni-2018).

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Author contribution

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.

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Table 1. Definition of symbols and acronyms.

Symbols and acronyms	Description	Dimensions *
AE	Assimilation efficiency	-
BPE	Biomass production efficiency	-
C	Carbon-mass	M L^{-2} or M
CSE	Carbon-storage efficiency	-
CUE	Carbon-use efficiency	-
CUE$_A$	Apparent carbon-use 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}
G	Growth	M L^{-2} T^{-1} or M T^{-1}
GGE	Gross growth efficiency	-
GPP	Gross primary productivity	M L^{-2} T^{-1}
I	Input	M L^{-2} T^{-1} or M 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}
Y_G	Growth yield	-

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

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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, growth yield, C use efficiency, growth efficiency	$\dfrac{\text{Biomass production}}{\text{C uptake}}$	(Payne 1970, van Bodegom 2007)(Monod, 1949)
	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	$\dfrac{\text{Biomass production}}{\text{Gross photosynthesis}}$	(Gifford, 1995)
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)
		U, G, R_h, EX	Substrate use efficiency	$\dfrac{\text{Biom. +exudate prod.}}{\text{C uptake}}$	(Schimel and Weintraub, 2003)
	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	$\dfrac{\text{NPP}}{\text{GPP}}$	(Cannell and Thornley, 2000; 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	$\dfrac{\text{Biomass production}}{\text{GPP}}$	(Lindeman 1942, Sterner and Elser 2002)

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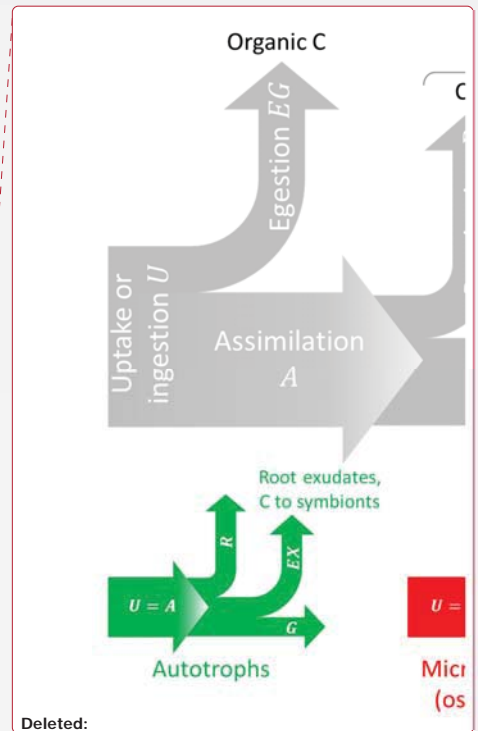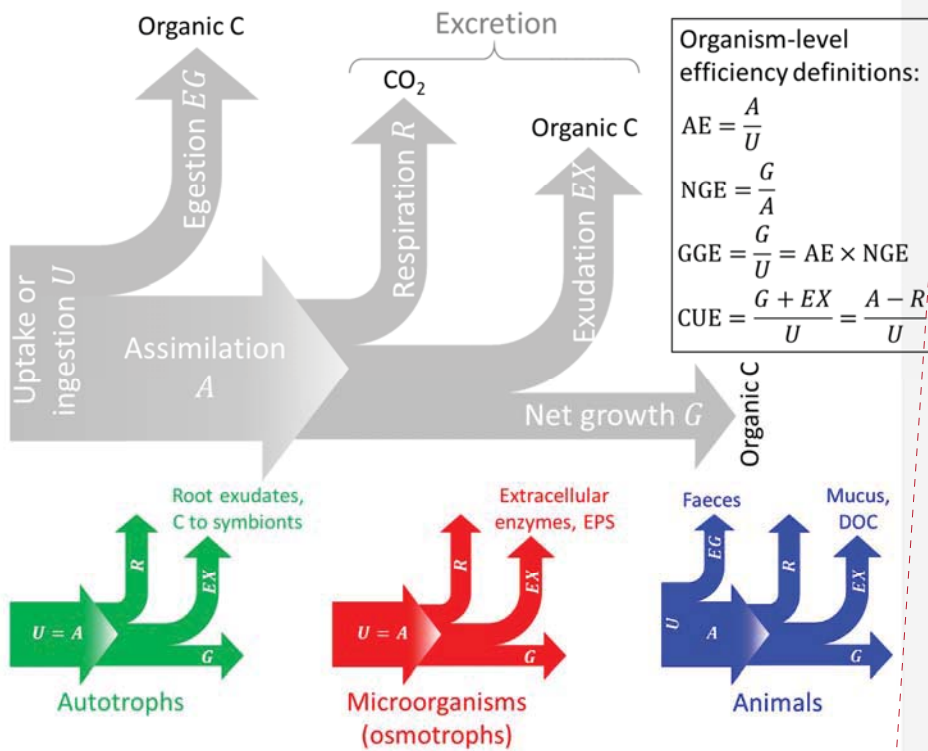| Watersheds (vegetation, soil, water bodies) | NECB, GPP | NA | $\dfrac{NECB}{GPP + F_{in}}$ | This paper |

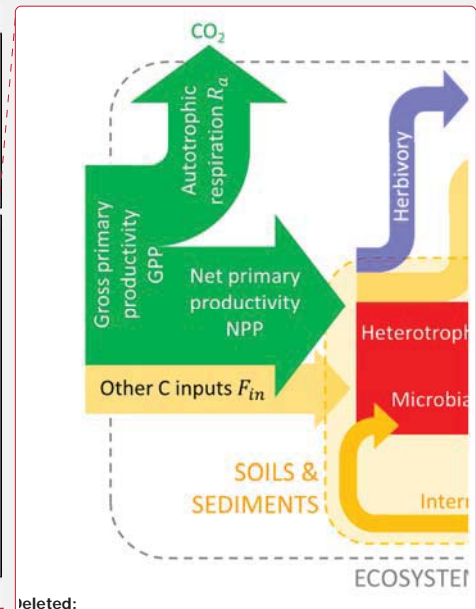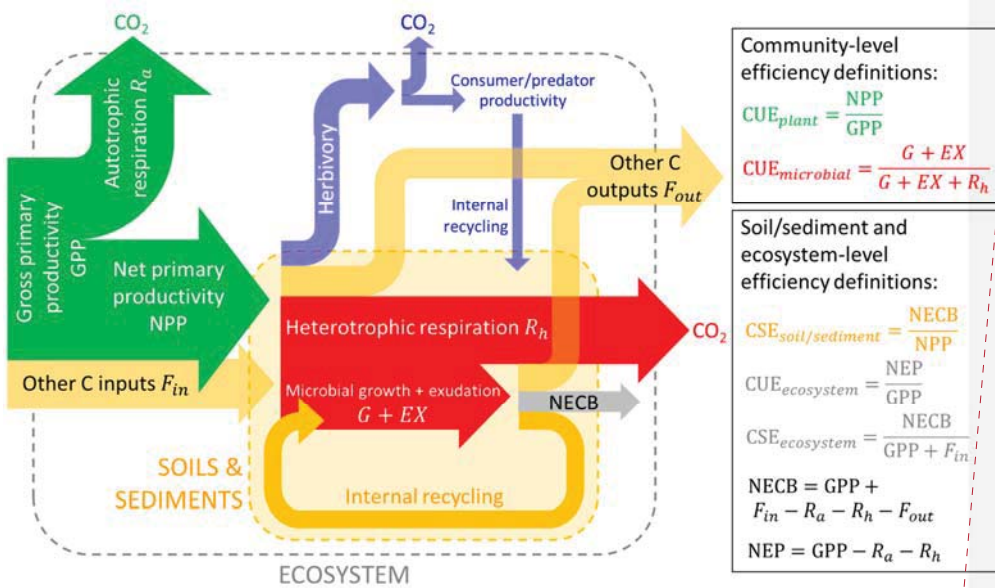* Symbols and acronyms refer to fluxes depicted in Fig. 1 and 2.

Table 3. Processes associated to the terms of Eq. (5) and (10) at different levels or organization (indicated as subscripts).

System	Inputs			Outputs			
	U	G	F_{in}	R	T	EX (and EG)	F_{out}
Leaves CUE_{leaf}	Gross photosynthesis	Net photosynthesis	-	Dark respiration, photo-respiration	Senescence		-
Micro-organisms $CUE_{microbial}$	Organic C uptake	Net biomass production	-	Growth, maintenance, overflow respiration	Cell decay, predation	Extracellular poly-saccharides and enzymes	-
Animals CUE_{animal}	Food ingestion	Net biomass production	-	Growth, maintenance, overflow respiration	Mortality, predation	Mucus and DOC exudation (and egestion)	-
Plants CUE_{plant}	Gross photosynthesis	Net primary productivity		Growth, maintenance	Mortality, senescence, herbivory	Root exudates, C export to symbionts	Loss due to disturbance, gaseous C other than CO_2
Soils CSE_{soil}	Litterfall and rhizodeposits ($\approx$NPP)	Net soil C balance	Through-fall	Heterotrophic respiration	-	-	Leaching, erosion
Sediments $CSE_{sediment}$	NPP ($\approx$0 in deep sediments)	Net sediment C balance	Deposition	Heterotrophic respiration	-	-	-
Ecosystems and watersheds $CUE_{ecosystem}$ (or $CSE_{ecosystem}$)	Gross primary productivity	Net ecosystem productivity	Lateral C inputs (CSE: deposition)	Autotrophic and heterotrophic respiration	-	-	Gaseous C other than CO_2 (CSE: leaching, erosion)

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Organism-level efficiency definitions:

$$AE = \frac{A}{U}$$

$$NGE = \frac{G}{A}$$

$$GGE = \frac{G}{U} = AE \times NGE$$

$$CUE = \frac{G + EX}{U} = \frac{A - R}{U}$$

1200 **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**
1205 **in other figures.**

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 or C-storage efficiencies (CUE or CSE) 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 CO_2 are denoted 'Other C inputs/outputs'. Colour codes for the different organisms and sub-systems are used also in other figures.

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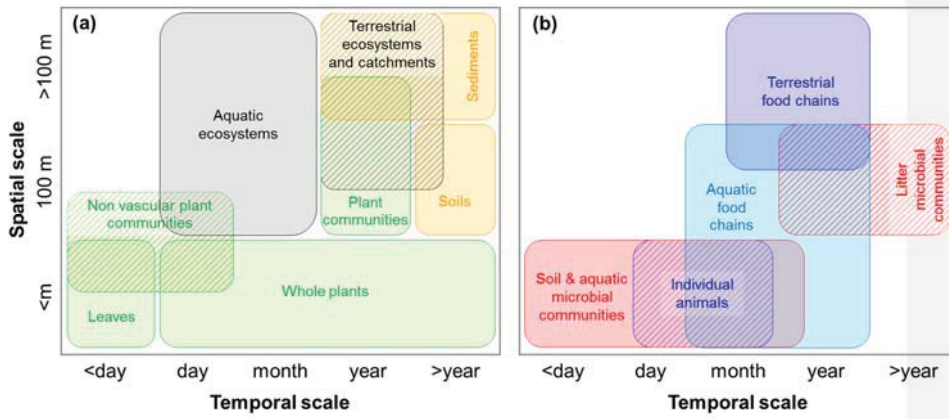
Figure 3. Illustration of typical spatial and temporal scales at which C fluxes are calculated to estimate CUE (or CSE) in various sub-systems. a) Scales typical of observations on vegetation, whole ecosystems, and soils/sediments; b) scales typical of observations on heterotrophic organisms and food chains. Colour codes are as in Fig. 2.

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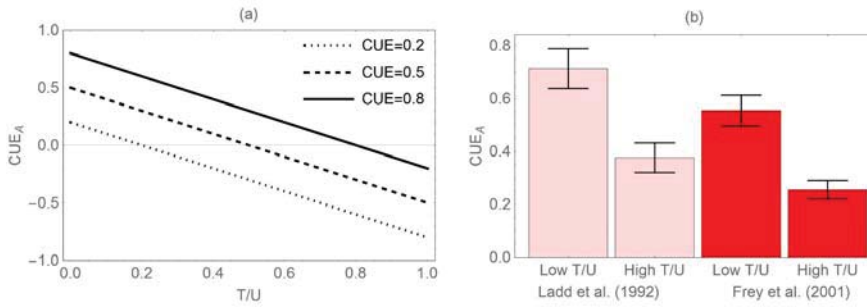
Figure 4. Effect of biomass turnover rate on the apparent C-use efficiency (CUE$_A$). (a) Theoretical relation between CUE$_A$ and the ratio of turnover rate over C uptake rate (Eq. (8), assuming negligible EX), for three values of the actual CUE. (b) Two examples of how high turnover rates cause a decrease in CUE$_A$ in empirical studies on soil microbial communities (Frey et al., 2001; Ladd et al., 1992). Lower turnover rates were caused by lower mortality in the first 3 days of incubation compared to the day 112 (Ladd et al., 1992), or by lower grazing in the first two days of incubation compared to days 7-8 (Frey et al., 2001). Error bars indicate standard errors of the mean (variability is across three soil types in Ladd et al. (1992) and across replicates and soil types in Frey et al. (2001)).

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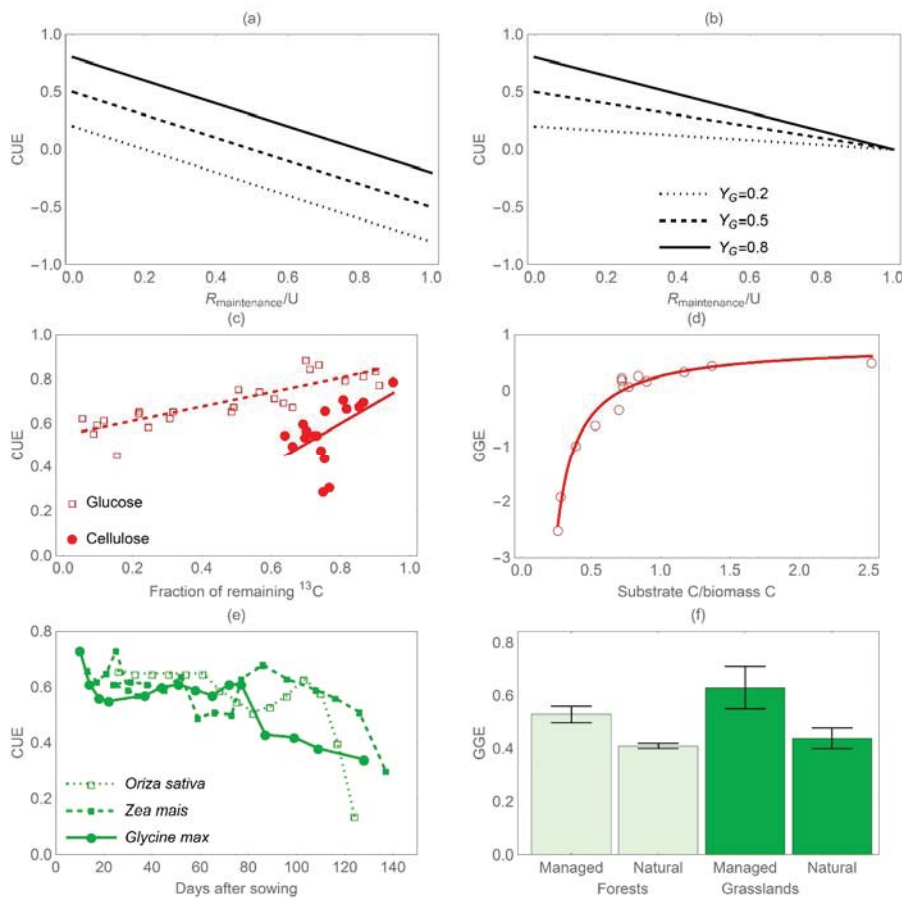
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Figure 5. Effect of maintenance respiration ($R_{maintenance}$) on C-use efficiency (CUE). Theoretical relations between CUE and the ratio of maintenance respiration over C uptake rate under two different assumptions: (a) priority to growth respiration, 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) during 12 (glucose) and 71 (cellulose) day incubations (Öquist et al., 2017) or (d) resource availability (as the ratio of salicylic acid 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) Significantly higher (*p*<0.05) GGE of managed, and thus more nutrient-rich, forests and grasslands (Campioli et al., 2015). In (c) to (e), CUE or GGE decrease as costs for maintenance respiration increase relative to growth respiration; in (f), GGE decrease when costs for symbiotic associations are higher (natural systems). 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.
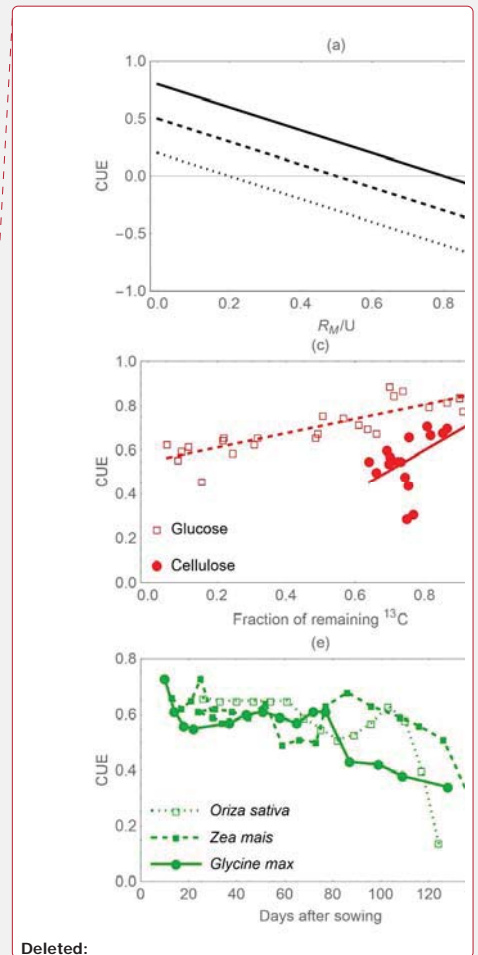
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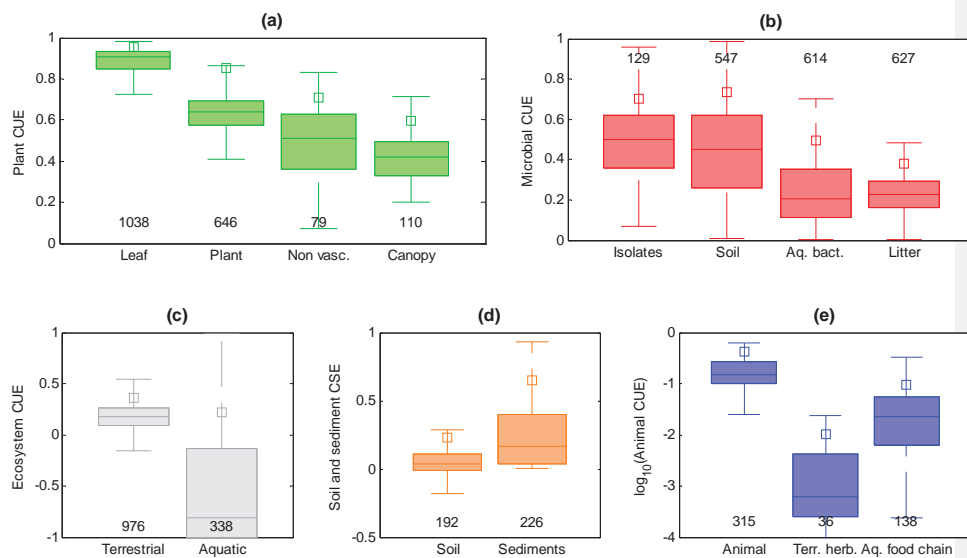
Figure 6. Patterns in C-use efficiency (CUE) across scales and levels of organization. (a) CUE of leaves and non-vascular plant communities, and GGE of whole plants and vascular plant communities; **(b)** CUE of microbial isolates, and communities of soil microorganisms, aquatic bacteria, and litter 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 and terrestrial herbivore communities, and C transfer efficiency of 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. Data sources are described in the Supplementary Information.
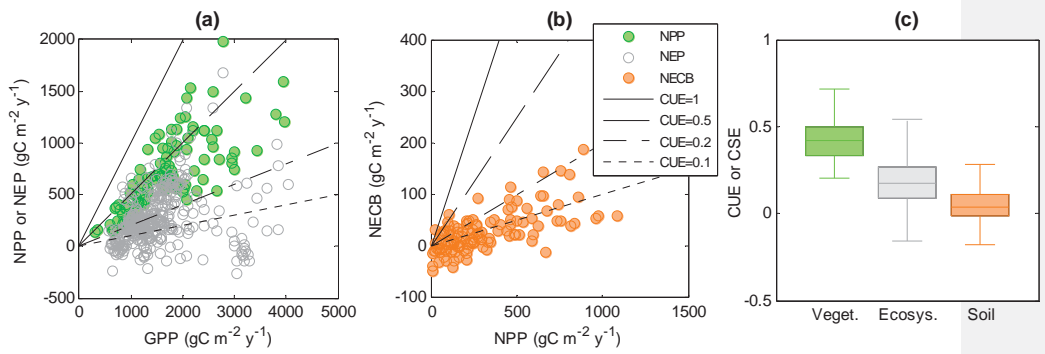
Figure 7. Relations between gross primary productivity (GPP) and (a) net primary productivity (NPP) or net ecosystem productivity (NEP), and (b) between NPP and net ecosystem C balance (NECB) in terrestrial systems. In these plots, CUE corresponds to the slopes of lines passing through the origin (four are shown for illustration). (c) Comparison of vegetation GGE, whole ecosystem CUE, and soils CSE (see also Fig. 2). Colour codes are as in Fig. 2. Data sources are described in the Supplementary Information.

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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,

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

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

CUE	Carbon-use efficiency	-
CUE_A	Apparent carbon-use efficiency	-
GGE	Gross growth efficiency	-
GPP	Gross primary productivity	$M\ L^{-2}\ T^{-1}$

Supplementary Information

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

Stefano Manzoni, Petr Čapek, Philipp Porada, Martin Thurner, Mattias Winterdahl, Christian Beer, Volker Brüchert, Jan Frouz, Anke M. Herrmann, Björn D. Lindahl, Steve W. Lyon, Hana Šantrůčková, Giulia Vico, Danielle Way

1 Estimating carbon-use and carbon-storage efficiencies

1.1 Leaves

Leaves are responsible for fixing atmospheric CO_2, thereby representing the entry points of C into terrestrial ecosystems. By measuring net photosynthesis and respiration, CUE at the leaf level can be defined as the ratio of net to gross photosynthetic rates,

$$CUE_{leaf} = \frac{Net\ photosynthesis}{Gross\ photosynthesis} = \frac{A_{net}}{A_{net}+R_{dark}+R_{photo}},\qquad(1)$$

where the net photosynthetic rate (A_{net}, also referred to as net CO_2 assimilation) is the difference between gross photosynthesis and the sum of photorespiration (R_{photo}) and mitochondrial respiration (R_{dark}). Photorespiration occurs when the photosynthetic enzyme Rubisco (which fixes CO_2) experiences non-saturating CO_2 conditions in the presence of O_2, as is the case for most plants in our current atmosphere. We therefore include photorespiration costs in the term gross photosynthesis in Eq. (1), as done in other studies (Way and Sage, 2008), although cannot account for that in our calculations due to data limitations. In leaves, mitochondrial respiration proceeds in both the dark and in the light, although respiration rates are often lower in the light than in the dark. As the phenomenon of light-suppression of respiration is poorly understood and leaf respiration in the light is difficult to measure (Tcherkez et al., 2017), we use dark respiration rates and assume that they represent respiration rates over a 24-hour period. Moreover, photorespiration is neglected in our calculations, because the compensation point was not reported in the dataset we used (Atkin et al., 2015), so that our estimates of leaf CUE are slightly overestimated.

1.2 Individual organisms (autotrophs and heterotrophs)

The balance of growth plus exudation and respiration defines the CUE of individual organisms (Eq. (5) in the main text),

$$CUE_{organism} = \frac{Net\ biomass\ production+exudation}{C\ uptake} = \frac{G+EX}{U} = 1 - \frac{EG+R}{U},\qquad(2)$$

where R includes all respiration components shown in Eq. (7) in the main text. The equalities in Eq. (2) show how CUE can be estimated from different combinations of observations: net biomass accretion (G) and exudation rate (EX), C consumption from the resource pool (U – organic C for heterotrophs or CO_2 for autotrophs), and respiration rate (R) (Geyer et al., 2016; Slansky and Feeny, 1977; Cannell and Thornley, 2000). While EX should be included in these calculations, it is generally neglected or implicitly considered as autotrophic respiration when calculating plant CUE. Neglecting exudation in terrestrial plants can lower the estimated NPP by up to 30%

(Clark et al., 2001), whereas the rate of exudate production by most heterotrophs is poorly constrained. Therefore, it is possible that neglecting exudation lowers estimated CUE of heterotrophs as it does for plants, but the extent of this error can be evaluated only after exudate production rates (extracellular polysaccharides and enzymes) are estimated.

For all organisms, when net biomass production and respiration are measured, cell turnover and other organic C losses during the incubation time are not accounted for, so that the estimated values should often be interpreted as 'apparent' CUE. This can be challenging when incubation times are long. For plants, gross rates of C uptake are estimated by summing up net photosynthesis measured during the day to the respiration rate obtained assuming that night and day respiration are comparable; if heterotrophic respiration is included in the measurements, it needs to be subtracted to isolate the autotrophic component (Wang et al., 2015) (see also Sect. 1.3). CUE of non-vascular vegetation, such as mosses and lichens, is defined in the same way as CUE of vascular plants with empirical estimates typically using respiration and gross photosynthesis to estimate CUE. Consequently, these studies share the same limitations noted for plants. Only few studies traced how much of newly acquired C is incorporated into biomass using isotopes (Street et al., 2013; Woodin et al., 2009; Lotscher et al., 2004).

1.3 Primary producer communities

CUE of plant communities can be defined as for individual plants, but using data at a larger scale (~100-1000 m) and covering the whole range of species and age classes in a certain community. In this case, the control volume conceptually comprises all plant organs including roots. It is thus virtually impossible to accurately measure all C exchange rates across the boundaries of this control volume, so that major assumptions on the contribution of autotrophs to measured net C fluxes have to be made (Clark et al., 2001). At this scale, production is defined by the net primary productivity (NPP) and C uptake by the gross primary productivity (GPP), so that (DeLucia et al., 2007; Zhang et al., 2009),

$$\text{CUE}_{plant\ community} = \frac{Net\ primary\ productivity}{Gross\ primary\ productivity} = \frac{\text{NPP}}{\text{GPP}} = 1 - \frac{R_a}{\text{GPP}}. \tag{3}$$

At the stand scale, GPP is obtained by flux partitioning from eddy covariance measurements of net ecosystem exchange (NEE) (Lasslop et al., 2010; Reichstein et al., 2005). NPP can be derived from the increase in biomass of the different biomass compartments (stem, branches, foliage, roots), but should also include the C allocated to understory, herbivory, reproductive organs, root exudates, volatile organic compounds and CH$_4$ emissions (Luyssaert et al., 2007; Clark et al., 2001). However, below-ground NPP as well as these latter C fluxes are extremely difficult to capture and thus often either ignored or very uncertain (Clark et al., 2001), creating some ambiguities in how CUE$_{plant\ community}$ is defined. As shown in Eq. (5) in the main text, plant community CUE should be calculated by including both net biomass increments and exudation rates. When only net biomass increments are available, the terms gross growth efficiency (GGE) or biomass production efficiency (BPE) are more accurate (as in Campioli et al., 2015; Vicca et al., 2012). BPE estimates are reported in an extensive global database for forest sites, including direct measurements, indirect estimates (derived from measurements of other C fluxes) and model results (Luyssaert et al., 2007). This dataset has been recently expanded to grasslands and croplands (Campioli et al., 2015) (data used in Fig. 5-7).

At the global scale, observation-based GPP products rely on either spatial extrapolation of diagnostic models relating site-level eddy covariance-derived GPP to climate, vegetation type and remote sensing indices (Beer et al., 2010), or on relations to the fraction of absorbed photosynthetic active radiation measured by satellite remote sensing (e.g., MODIS, with resolution ~1000 m) (Zhao et al., 2005). Global observation-based NPP products in turn are solely available from combining satellite-based GPP estimates with model assumptions on biomass allometry and autotrophic respiration (Tum et al., 2016; Zhao and Running, 2010).

In addition to the existing dataset for vascular plant communities, we also estimated CUE for non-vascular vegetation using reported respiration and photosynthetic rates. In productive forest and grassland ecosystems, non-vascular vegetation usually contributes only a small part to total carbon uptake. Exceptions are high values of up to 60% at high latitudes (Turetsky et al., 2010). Because of this small contribution, it is impractical to estimate CUE of non-vascular vegetation by methods such as eddy covariance. In less productive drylands where non-vascular vegetation may be the main primary producers, samples of complete crusts can be collected in the field and the CUE of these communities can be derived from measured net photosynthesis and dark respiration in the laboratory (see references in Table S2).

1.4 Microbial communities

While conceptually similar to the definition for individual organisms, interpreting CUE at the whole microbial community level (in either terrestrial or aquatic systems) is complicated by the presence of inactive organisms and by the co-occurrence of a range of life history strategies with their potentially different CUE (Geyer et al., 2016; del Giorgio and Cole, 1998). CUE is estimated typically by measuring (at least) two among the C fluxes relevant for microbial C budgets: substrate consumption (assumed to be equal to C uptake; i.e., neglecting losses of depolymerized C before uptake by microorganisms), net microbial growth, and respiration rates (Manzoni et al., 2012). These C exchanges are generally measured under controlled conditions in relatively small incubation systems (<1 L volume) and in transient conditions. A substrate (often isotopically-labelled) is generally added to trace C uptake into biomass and thus determine the changes in C pools required to estimate CUE. In marine sediments, ^{3}H, ^{14}C, or ^{13}C-uptake experiments are conducted to estimate microbial growth rates, but application of this technique in sediments is challenging, and the contribution of biomass turnover is poorly constrained (an issue shared with measurements in soil).

The concentration and choice of substrate (more or less similar to compounds used in natural conditions) and the length of the incubation period affect the obtained CUE (see Sect. 4.1 in the main text). Labile substrates and more generally higher C concentrations result in higher CUE values (Frey et al., 2013; Öquist et al., 2017; del Giorgio and Cole, 1998; Bolscher et al., 2017), while increasing incubation time from a day to a week or more results in lower apparent CUE, as necromass is recirculated and used (Ladd et al., 1992; Öquist et al., 2017). Previous reviews discuss these methodological issues in depth (Geyer et al., 2016; Sinsabaugh et al., 2013; del Giorgio and Cole, 1998).

Microbial exudation rates cannot be readily measured in soils and available evidence of the fate of C in extracellular products is limited. Even though the standing extracellular polysaccharide mass can be comparable to that of the microbial biomass (Marchus et al., 2018), without knowing the turnover rate of these extracellular compounds, production rates cannot be estimated. In contrast, the turnover rate of extracellular enzymes has been estimated (Allison, 2006), but not their standing mass, which again hampers our understanding of production

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rates. In one article, ^{14}C has been used to identify extracellular metabolites, showing that in laboratory conditions their accumulation is negligible in aerobic soil samples, but not in permanently anaerobic ones (Šantrůčková et al., 2004). Therefore, it is difficult to quantify potential errors in CUE estimates based on biomass increments, but neglecting exudation rates (i.e., when CUE is approximated by GGE), compared to estimates based on substrate uptake and respiration rates (Eq. (5) in the main text).

1.5 Food webs

The efficiency of C (and energy) transfer in terrestrial and aquatic food webs has been defined as the ratio of C used at a certain trophic level and the C produced at a lower level (Dickman et al., 2008; Downing et al., 1990; Lindeman, 1942; McNaughton et al., 1989). These transfer efficiencies are not defined as for individual organisms because they consider inputs to a food web and biomass increments in a single component of the food web, but we include them here for completeness. The scale at which C transfer efficiencies are calculated varies widely, ranging from small-scale laboratory to broad-scale field studies (Fig. 3). In terrestrial systems, where NPP is the main C input to food-webs, the efficiency of herbivore production is evaluated with respect to NPP (McNaughton et al., 1989). In aquatic systems, allochtonous C inputs have been typically neglected, and the efficiency of herbivore or predator production is also estimated with respect to primary productivity.

1.6 Soils and sediments

The efficiency of C storage in soils has been studied in the context of climate change mitigation strategies, aiming to understand how much of the C added to a soil can be stored there and potentially sequestered (Stewart et al., 2007). The C storage efficiency of soils (CSE_{soil}) is defined as the ratio of the net soil C balance and the total C inputs from vegetation (~NPP) and soil amendments. As such, CSE_{soil} can be positive when soils accumulate C or negative when C losses are larger than inputs. With this definition, and assuming for simplicity that NEP≈NECB, CSE_{soil} can be related to ecosystem and vegetation CUE (Section 1.7) as $CUE_{ecosystem} = CSE_{soil} \times CUE_{vegetation}$.

C fluxes to quantify CSE_{soil} are measured at the plot- to field-scale, analogous to $CUE_{ecosystem}$, but because soil organic matter changes slowly, CSE_{soil} is generally defined over decades in specifically designed long-term experiments set up in agricultural systems where vertical C inputs are controlled and manipulated (but again lateral C fluxes are neglected; see references in Table S2). In these experiments, annual C inputs are measured and long-term C storage changes are estimated from repeated SOC measurements – thus, this method implicitly requires a (long) time frame over which a time-integrated CSE is calculated.

A conceptually similar CSE can be defined for lake and marine sediments and is often referred to as organic C burial efficiency (or preservation efficiency), as the ratio between the rates of C burial and of deposition at the sediment surface ($CSE_{sediment}$) (Alin and Johnson, 2007; Canfield, 1994; Hedges and Keil, 1995). In sediment CSE calculations, benthic photosynthesis is ignored in most environments (despite shallow-water ecosystems being among the most productive in the world), assuming that the export of C from the photic zone dominates C accumulation. Organic C accumulation in sediments is often only measurable over multi-year time-scales by ^{210}Pb dating, which fails to account for the initial rapid degradation of organic material at the sediment surface. As for soils, this method yields a time-integrated CSE (rather than instantaneous). An alternative definition involves primary productivity instead of C deposition, which underestimates CSE because it neglects

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C removal via respiration in the photic zone and during sedimentation (Azam and Malfatti, 2007; Ducklow et al., 2001). An instantaneous burial efficiency can be determined by measurements of ^{210}Pb-based C accumulation rates minus respiration rates measured through oxygen consumption. Moreover, all these methods share similar issues; primarily, they focus on vertical fluxes and tend to neglect lateral transport of C, in particular as DOC (Seiter et al., 2005; Alperin et al., 1994).

1.7 Ecosystems

At the ecosystem level, both CUE of the biotic components and CSE can be defined. When focusing on the biotic components, the only input $U = \text{GPP}$ and the only output is respiration (assuming exudates are re-cycled), which comprises autotrophic and heterotrophic terms. Net ecosystem productivity (NEP) is thus defined as the difference between GPP and the total respiration ($R = R_a + R_h$), and ecosystem CUE can be written as,

$$\text{CUE}_{ecosystem} = \frac{Net\ ecosystem\ productivity}{Gross\ primary\ productivity} = \frac{\text{NEP}}{\text{GPP}} = 1 - \frac{R}{\text{GPP}} = 1 - \frac{R_a + R_h}{GPP} = \text{CUE}_{plant\ community} - \frac{R_h}{\text{GPP}}, \quad (4)$$

where the first equality is used for empirical estimation of ecosystem CUE (Fernandez-Martinez et al., 2014), whereas the last equality links ecosystem CUE to the vegetation CUE (=NPP/GPP) and the heterotrophic respiration to GPP ratio. When including abiotic components and thus lateral abiotic fluxes, Eq. (10) in the main text can be used to obtain,

$$\text{CSE}_{ecosystem} = 1 - \frac{R_a + R_h + F_{out}}{\text{GPP} + F_{in}}. \quad (5)$$

The scale at which terrestrial ecosystem-level C fluxes are measured is comparable to that for plant communities (~100-1000 m), but the control volume extends to include soils (generally down to the rooting depth) (Chapin et al., 2006). C fluxes are generally obtained from eddy covariance systems that measure vertical net CO_2 exchanges (NEE); GPP is then inferred by adding total ecosystem respiration (based on night-time C exchanges) to the day-time C fluxes. While the eddy covariance approach provides fluxes at sub-daily time scales, often these are aggregated at the annual time scale in ecosystem-level CUE and CSE estimates. Because this approach measures vertical CO_2 exchanges, it neglects lateral transfer of C in both the atmosphere and the water bodies (see Sect. 1.8), and exchanges occurring in gaseous forms other than CO_2 (Chapin et al., 2006).

In aquatic systems, net oxygen fluxes are often used to infer C fluxes and CUE (Hoellein et al., 2013; Glud, 2008). Measurements are conducted on small samples (~0.1-1 L), but averaged spatially to have representative values for the water body under investigation, or by eddy covariance (over spatial scales ~100-1000 m) (Berg et al., 2003). Respiration is calculated from oxygen consumption at night, which is then used to correct the daytime net oxygen production to estimate gross primary productivity. Moreover, as for terrestrial ecosystems, this approach neglects allochthonous CO_2 contributions; e.g., from groundwater (Hall and Tank, 2005). Most freshwater bodies are prevalently heterotrophic, because of large allochthonous inputs of organic C that is decomposed locally (Duarte and Prairie, 2005; Hoellein et al., 2013). As a consequence, NEP is often strongly negative (large $\frac{R_h}{\text{GPP}}$ in Eq. (4)), leading to negative values of $\text{CUE}_{ecosystem}$, despite all organisms having positive CUE values. When accounting for C transport in and out of a heterotrophic system (Eq. (5)), estimated CSE is expected to increase because $F_{out} < F_{in}$, which reduces the numerator with respect to the denominator in the last term of Eq. (5). As a result, $\text{CSE}_{ecosystem} > \text{CUE}_{ecosystem}$, although $\text{CSE}_{ecosystem}$ remains negative as long as the ecosystem is a net source of C.

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In the photic zone of marine ecosystems, a conceptually similar efficiency is defined – the biological pump efficiency, which represents the ratio of C exported outside the euphotic zone (operationally defined at 100 m depth) over the net primary productivity (Ducklow et al., 2001; Volk and Hoffert, 1985). The biological pump efficiency is estimated from independent measurements of net primary productivity (phytoplankton uptake minus respiration over a 24-hour period) and C export either from sediment traps or ^{234}Th flux-based measurements (Boyd and Trull, 2007; Giering et al., 2017; Le Moigne et al., 2015). This efficiency increases when less C is re-mineralized in the euphotic zone via decomposition and consumption by the aquatic food web (Azam and Malfatti, 2007; Ducklow et al., 2001). However, not all C exported below the euphotic zone is stored, because a potentially large fraction is re-mineralized in the upper mesopelagic zone (< 300 m water depth) (Buesseler and Boyd, 2009; Wakeham et al., 1997). A better measure of C storage efficiency for marine systems is therefore the organic carbon burial efficiency in sediment (Sect. 1.6). However, in particular in shelf systems, resuspension and lateral transport of deposited organic material to the continental slope constitute an important loss component (Inthorn et al., 2006).

Figure S1a illustrates the relations between C export rates (either as litter production or C export below the euphotic zone) and net primary productivity in terrestrial and aquatic ecosystems. The ratios of these C export and NPP fluxes define C export efficiencies (or biological pump efficiency for oceanic systems), shown in Fig. S1b. Terrestrial systems have much higher efficiencies than aquatic systems in general and in particular than oceanic systems ($p<0.05$), indicating that herbivory or other C loss pathways are more effective in aquatic systems at removing biomass that would be otherwise exported to the decomposition pathway.

1.8 Watersheds

Watersheds represent naturally-defined control volumes for water fluxes and are convenient also for C budget calculations because they allow measuring lateral outputs of dissolved C at the watershed outlet. At the watershed scale, C inputs are given by terrestrial and aquatic GPP and atmospheric deposition (which we neglect for simplicity) and C outputs include heterotrophic and autotrophic respiration (as in Sect. 1.7), but also lateral abiotic losses via dissolved organic and inorganic C transport in rivers and groundwater (denoted by F_{out}). Thanks to the nature of a watershed, C flows by advection in dissolved phase are limited to losses from the system, so that abiotic C inputs can be neglected compared the to the other C fluxes. Therefore, the watershed-scale CSE can be defined as (from Eq. (10) in the main text and the definition of $CUE_{ecosystem}$ in Eq. (4)),

$$CSE_{watershed} = \frac{NECB}{GPP} = 1 - \frac{R+F_{out}}{GPP} = CUE_{ecosystem} - \frac{F_{out}}{GPP}; \tag{6}$$

where the net ecosystem carbon balance is evaluated in the whole watershed. Eq. (6) illustrates that increased abiotic losses of C decrease $CSE_{watershed}$ with respect to the efficiency of the biotic component of the system ($CUE_{ecosystem}$). Also, the lateral abiotic losses are particularly high at times when GPP is low, such as during high precipitation/low radiation events (Öquist et al., 2014) or during snow-melt in cold environments (Finlay et al., 2006). There are only a few watersheds with long-term monitoring of both vegetation-atmosphere C exchanges and C transport in water bodies, in which $CSE_{watershed}$ can be estimated (see references in Table S2).

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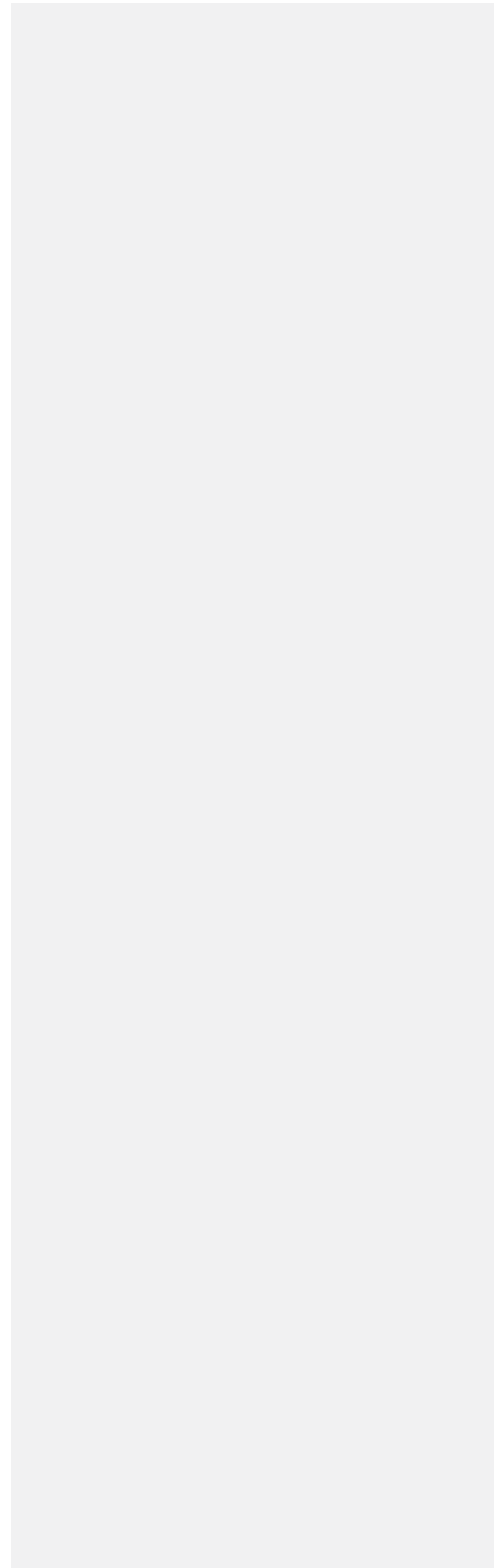
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Table S1. Definition of symbols and acronyms used in the Supplementary Information. Subscripts indicating the system under consideration are added to acronyms (*leaf*, *organism*, *plant community*, *autotroph*, *ecosystem*, *soil*, *sediment*), but are not included in this table.

Symbols and acronyms	Description	Dimensions *
AE	Assimilation efficiency	-
A_{net}	Net photosynthesis	M L^{-2} T^{-1}
BPE	Biomass production efficiency	-
C	Carbon-mass	M L^{-2} or M
CSE	Carbon-storage efficiency	-
CUE	Carbon-use efficiency	-
CUE$_A$	Apparent carbon-use 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}
GGE	Gross growth efficiency	-
GPP	Gross primary productivity	M L^{-2} T^{-1}
I	Input	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}
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_{dark}	Dark respiration	M L^{-2} 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}
R_{photo}	Photorespiration	M L^{-2} 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.

Deleted: I

Deleted: Input

Deleted: M L^{-2} T^{-1}

Deleted: C

Deleted: Carbon-mass

Deleted: M L^{-2} or M

Deleted: CSE

Deleted: Carbon-storage efficiency

Deleted: -

Deleted: CUE   ... [1]

685   **Table S2. Data sources (online databases were last accessed on November 17th, 2017).**

System	Figures	Sources	Dataset
Leaves	6a	(Atkin et al., 2015)	Existing dataset (GlobResp database, https://www.try-db.org/TryWeb/Data.php)
Whole plants	5e, 6a	(Wang et al., 2015; Atkin et al., 1996; Atkin et al., 2007; Dillaway and Kruger, 2014; Frantz and Bugbee, 2005; Frantz et al., 2004; Gifford, 1995; Loveys et al., 2002; Nemali and van Iersel, 2004; Tjoelker et al., 1999; van Iersel, 2000, 2003; Yamaguchi, 1978; Yokota and Hagihara, 1998; Ziska and Bunce, 1998; Gifford, 2003; Lotscher et al., 2004; Poorter et al., 1990)	Original compilation*
Non-vascular plant communities	6a	(Green et al., 1998; Lange, 2002; Lange et al., 1998; Lange et al., 2000, 2004; Lange et al., 1977; Palmqvist and Sundberg, 2000; Pannewitz et al., 2005; Sundberg et al., 1997; Tretiach and Geletti, 1997; Uchida et al., 2006; Wagner et al., 2013; Uchida et al., 2002; Palmqvist, 2002; Kappen et al., 1989; Oechel and Collins, 1976; Brostoff et al., 2002, 2005; Goulden and Crill, 1997; Jeffries et al., 1993; Lange et al., 1997a; Lange et al., 1993; Lange et al., 2006; Lange et al., 1997b; Lange et al., 1992; Street et al., 2013; Swanson and Flanagan, 2001; Woodin et al., 2009; Yoshitake et al., 2010; Zaady et al., 2000; Büdel et al., 2013; Lange and Green, 2002, 2004; Street, 2011)	Original compilation based on existing synthesis papers (Lenhart et al., 2015; Porada et al., 2013)*
Vascular plant communities	5f, 6a, 7	(Campioli et al., 2015)	Existing dataset (https://www.nature.com/articles/ngeo2553#supplementary-information)
Microbial isolates	6b	(Gommers et al., 1988; Lehmeier et al., 2016; Min et al., 2016; Roels, 1980; Collado et al., 2014; Schmidt et al., 2005; Wakelin and Forster, 1997)	Original compilation including previous synthesis papers
Terrestrial and aquatic microorganisms	4b, 5c, 5d, 6b	(Manzoni et al., 2017)	Existing dataset (http://bolin.su.se/data/Manzoni-2017)
Animals	6e	(Manzoni et al., 2017)	Existing dataset (http://bolin.su.se/data/Manzoni-2017)
Terrestrial ecosystems	6c, 7	(Luyssaert et al., 2007; Luyssaert et al., 2009)	Existing dataset (http://dx.doi.org/10.3334/ORNLDAAC/949)

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Aquatic ecosystems	6c	(Hoellein et al., 2013)	Existing dataset (http://onlinelibrary.wiley.com/doi/10.4319/lo.2013.58.6.2089/abstract)
Terrestrial food chains	6e, S2	(McNaughton et al., 1989; Cebrian and Lartigue, 2004)	Previous synthesis papers
Aquatic food chains	6e, S2	(Adams et al., 1983; Dickman et al., 2008; Downing et al., 1990; Iverson, 1990; Lefebure et al., 2013; Liang et al., 1981; Rock et al., 2016; Rowland et al., 2015; Cebrian and Lartigue, 2004; Dunne et al., 2005)	Original compilation including previous synthesis papers*
Soils	6d, 7	(Hua et al., 2014; Liang et al., 2016; Purakayastha et al., 2008; Tan et al., 2014; Yan et al., 2013; Zhang et al., 2015; Zhang et al., 2010a; Zhang et al., 2012; Zhao et al., 2016; Poeplau et al., 2017; Poffenbarger et al., 2017; Zhang et al., 2017; Parton and Rasmussen, 1994; Paustian et al., 1992)	Original compilation*
Sediments	6d	(Alin and Johnson, 2007; Ferland et al., 2014; Sobek et al., 2009; Canfield, 1994; Hartnett et al., 1998; Hedges and Keil, 1995)	Original compilation including previous synthesis papers
Watersheds	Results presented in the text	(Gielen et al., 2011; Leach et al., 2016; Olefeldt et al., 2012; Peichl et al., 2014; Waddington and Roulet, 2000; Öquist et al., 2014; Zhou et al., 2013; Dinsmore et al., 2010; Helfter et al., 2015; Zhang et al., 2010b)	Original compilation*

690 * Datasets available from the Bolin Centre Database (https://bolin.su.se/data/Manzoni-2018).

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Table S3. Comparisons of definitions of biological C-use efficiencies for plants and soil microorganisms.

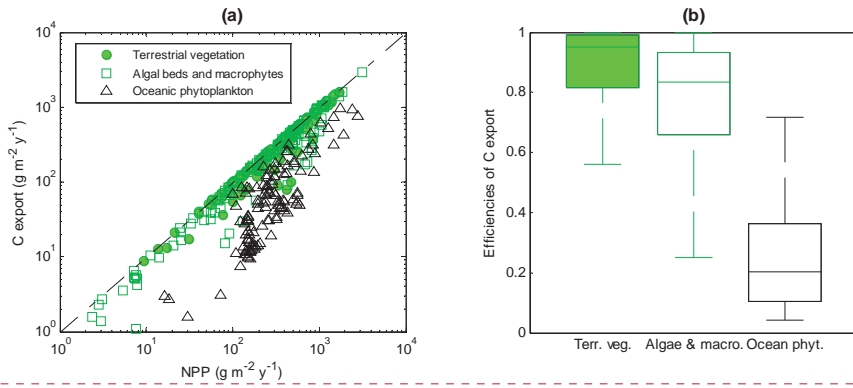| Definitions in this work	Context	Alternative definitions in published literature	Source
$CUE_A = 1-O/I$	Soil microbial communities	Ecosystem-scale efficiency of microbial biomass synthesis and recycling of necromass/exudates (CUE_E)	(Eq. 2 in Geyer et al. 2016)
$GGE = G/U$	Animals and microorganisms	Gross growth efficiency (GGE)	(Sterner and Elser 2002)
	Microbial communities	Carbon use efficiency (CUE)	(Eq. 2 in Manzoni et al. 2012)
	Soil microbial communities	Community-scale efficiency of microbial biomass synthesis (CUE_C)	(Eq. 1 in Geyer et al. 2016)
	Individual plants	Carbon use efficiency (CUE)	(Gifford 1995)
	Plant communities	Biomass production efficiency (BPE)	(Campioli et al. 2015)
$CUE = 1-R/U$	Soil microbial communities	Community-scale efficiency of microbial biomass synthesis when $EX \approx 0$ (also denoted as CUE_C)	(Figure 3 in Geyer et al. 2016)
	Plant communities	Carbon use efficiency (CUE = NPP/GPP)	(Cannell and Thornley 2000)

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Figure S1. Comparison of the efficiencies of C export (exported C/primary production) among terrestrial and aquatic ecosystems. (a) Relation between C export rate and net primary productivity; (b) box plot of C-export efficiencies across ecosystem types. Data for terrestrial vegetation and algal beds/macrophytes is from Cebrian and Lartigue (2004); data for oceanic phytoplankton is from Dunne et al. (2005).

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