General Response to Referees' Comments

Three anonymous referees have provided generally positive comments on our manuscript, with some constructive critiques that we plan to address as explained below (responses are written in *italic*; modified text in quotation marks). The three main comments are as follows:

- Reviewer #1: ambiguous definition of C-use efficiency (CUE) for organisms and communities. The reviewer correctly argues that CUE should be defined as 1-respiration rate/uptake rate. This means that biological products such as exudates should be accounted for in the CUE definition, differently from gross growth or biomass production efficiency in which net biomass increments only are accounted for. We will revise our definition according to the reviewer's suggestion.
- Reviewer #2: lacking discussion on human impacts on ecosystem scale efficiencies. This is an excellent suggestion as it prompted us to generalize the definition of C storage efficiency (CSE). We will include anthropogenic C fluxes in our definition of CSE and comment on the role of ecosystem management as a driver of change for CSE.
- Reviewer #3: lack of clarity in some definitions. We will revise the text to clarify ambiguous definitions, and change Table 3 to indicate which components of the C cycle represent inputs and outputs in each of the systems/scales considered.

Detailed responses are reported in the individual rebuttal letters.

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.

We agree that we did not present a very extensive data analysis (we will add some clarifications to this regard in Section 3 "Data collection and analysis"; see response to Reviewer 2). Our aim is more modest – we show variability in the data and some patterns that are illustrative of underlying dynamics or drivers and, as also stated above, the main novelty is represented by the synthesis of definitions and the comparison of many conceptually related type of data.

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.

Thanks for pointing to these issues, which we will address as explained below.

*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.

The acronym CUE was first used in plant science in the mid-1990s and later it has been proliferating across disciplines (see Table 2). Therefore, given the widespread use of this acronym, it seems appropriate to compare the different definitions proposed and choose one that represents the conceptual consensuses across these disciplines. For this reason, we would prefer to avoid introducing new terms, but we also acknowledge that 'imposing' a single term may create confusions (as also pointed out by Reviewer 1). We will give a more rigorous definition of CUE as opposed to gross growth efficiency and biomass production efficiency (please see also to this regard our response to Reviewer 1). By defining CUE as the ratio of all biosynthesis products (new biomass and compounds that will be released e.g., as exudates), previous definitions become comparable. In fact, in plant science and in papers on ecosystem C fluxes, CUE is defined as NPP/GPP, consistent with our revised definition. The microbial CUE is also already defined in this way by some (but not all) authors, but given the probably lower role of microbial exudates compared to plant exudates (though evidence is lacking), the discrepancy is mainly semantic. Hence the revised definition does not contradict previous work, but offers an improvement that can be embraced in future publications.

To this end, we will revise the paragraph on 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),

$$CUE = \frac{G+EX}{U} = 1 - \frac{EG+R}{U}. \quad (5)$$

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

$$\frac{dC}{dt} = CUE \times U - EX - T. \qquad (6)$$

With this definition, CUE represents the fraction of C taken up allocated to biosynthesis (biomass and products that will be eventually 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 is motivated by the clear fitness advantage these products have for the organism…"

*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?

The structure suggested by the Reviewer – extensive discipline-specific definitions before the theory section – is indeed a good alternative to our structure. However, it has a shortcoming: it requires defining many terms that would appear as conceptually different (because they are called in different ways across disciplines). Presenting first a general theory allows avoiding this shortcoming. Extensive definitions and discussions on how C fluxes are measured and interpreted at the various scales is presented in the Supplementary Information. Unfortunately, we cannot include them in the main text also due to space limitations; examples are also provided in Figures 4 and 5.

We will implement the suggestion to clarify what 'input' and 'output' represent across scales. Specifically, we will revise 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 will change 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.

AE, NGE, GGE, and ecosystem CUE are all terms currently in use. In particular, the first three acronyms are typically adopted in the literature on animal physiology (Sterner and Elser 2002). The term 'apparent' in association with CUE or equivalent efficiencies is also already in use to indicate when the efficiency is estimated from data, but the obtained values are not 'true' efficiencies due to confounding factors (Hagerty et al. 2014). On purpose, we present all the definitions currently in use and compare them conceptually and mathematically.

We are sorry that the way ecosystem CUE – a term already in use as well (Fernandez-Martinez et al. 2014) – is defined in our manuscript was not clear. Ecosystem CUE = NEP/GPP, as reported in Table 2 and Figure 2 in the main text, and Section 1.7 in the Supplementary Materials. Perhaps, part of the confusion arises because the ratio NEP/GPP refers to the biotic component of C exchanges at the ecosystem scale, but we also define a C storage efficiency *that includes abiotic (or anthropogenic) C exchanges. The relevant explanations are reported in section 1.7 of the Supplementary Materials:*

"At the ecosystem level, both CUE of the biotic components and CSE can be defined. When focusing on the biotic components, the only input $U = GPP$ 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,

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

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,

$$CSE_{ecosystem} = 1 - \frac{R_a + R_h + F_{out}}{GPP + F_{in}}. \quad (2)"$$

*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 agree that turnover has different meaning in different context, but in all cases it represent a loss of viable biomass due to senescence, damage, or herbivory. Mathematically, it might cause negative 'apparent' CUE when growth is lower than biomass losses. The paper by Clark et al. (2001) describes how NPP can be estimated. Turnover terms are considered in that paper because of the methodology used to measure net biomass increments over a given interval. This methodology does not capture organic material that was fixed but lost during that period. Hence, NPP remains defined as GPP minus autotrophic respiration, and not GPP minus respiration plus turnover. However, empirical estimates of NPP require accounting for C loss via various turnover mechanisms to correctly count the actual biomass increment. Therefore, unless we misinterpreted the comment, we would prefer not to make changes to the manuscript in response to this comment.

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.

This is a good suggestion, which we implemented. The Conclusions will be almost completely rewritten to incorporate the main closing arguments on both terminological issues raised by the other reviewers, and trends from our data synthesis:

"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 CUE, Eq. (8)), and gross growth efficiency (Fig. 1). 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 will re-write this sentence to clarify that crops (not a generic "plant" as stated in the original manuscript) stop photosynthesizing and therefore CUE decreases:

"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 will be 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.

References

Fernandez-Martinez, M., S. Vicca, I. A. Janssens, J. Sardans, S. Luyssaert, M. Campioli, F. S. Chapin Iii, P. Ciais, Y. Malhi, M. Obersteiner, D. Papale, S. L. Piao, M. Reichstein, F. Roda, and J. Penuelas. 2014. Nutrient availability as the key regulator of global forest carbon balance. Nature Clim. Change **4**:471–476.

Hagerty, S. B., K. J. van Groenigen, S. D. Allison, B. A. Hungate, E. Schwartz, G. W. Koch, R. K. Kolka, and P. Dijkstra. 2014. Accelerated microbial turnover but constant growth efficiency with warming in soil. Nature Climate Change **4**:903-906.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry. The biology of elements from molecules to the biosphere. Princeton University Press, Princeton and Oxford.