



Supplement of

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

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1 Estimating carbon-use and carbon-storage efficiencies

1.1 Leaves

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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,

 $CUE_{leaf} = \frac{Net \ photosynthesis}{Gross \ photosynthesis} = \frac{A_{net}}{A_{net} + R_{dark} + R_{photo}},$ (S1)

where the net photosynthetic rate (A_{net} , also referred to as net CO₂ 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 CO₂) experiences non-saturating CO₂ conditions in the presence of O₂, as is the case for most plants in our current atmosphere. We therefore include photorespiration

- 10 costs in the term gross photosynthesis in Eq. (S1), 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-
- 15 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),

$$CUE_{organism} = \frac{Net \ biomass \ production + exudation}{C \ uptake} = \frac{G + EX}{U} = 1 - \frac{EG + R}{U}, \tag{S2}$$

- where *R* includes all respiration components shown in Eq. (7) in the main text. The equalities in Eq. (S2) 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 CO₂ 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.
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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

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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).

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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),

$$CUE_{plant\ community} = \frac{Net\ primary\ productivity}{Gross\ primary\ productivity} = \frac{NPP}{GPP} = 1 - \frac{R_a}{GPP}.$$
(S3)

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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 CH₄ 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 equivalently biomass production efficiency (BPE) are more accurate (as in Campioli et al., 2015; Vicca et al., 2012). GGE 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

65 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 nonvascular 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

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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, ³H, ¹⁴C, or ¹³C-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
- 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
- 95 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

- 100 estimated (Allison, 2006), but not their standing mass, which again hampers our understanding of production rates. In one article, ¹⁴C 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
- 105 uptake and respiration rates (Eq. (5) in the main text).

issue shared with measurements in soil).

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

110 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

- 120 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 \approx NECB, CSE_{soil} can be related to ecosystem and vegetation CUE (Section 1.7) as $CUE_{ecosystem} \approx CSE_{soil} \times CUE_{vegetation}$.
- 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.
- 130 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
- 135 dominates C accumulation. Organic C accumulation in sediments is often only measurable over multi-year timescales by ²¹⁰Pb 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 C removal via respiration in the photic zone and during sedimentation (Azam and Malfatti, 2007; Ducklow et al.,
- 140 2001). An instantaneous burial efficiency can be determined by measurements of ²¹⁰Pb-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

145 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,

$$CUE_{ecosystem} = \frac{Net \ ecosystem \ productivity}{Gross \ primary \ productivity} = \frac{NEP}{GPP} = 1 - \frac{R}{GPP} = 1 - \frac{R_a + R_h}{GPP} = CUE_{plant \ community} - \frac{R_h}{GPP},$$
(S4)

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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; Eq. (S3)) 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,

$$CSE_{ecosystem} = 1 - \frac{R_a + R_h + F_{out}}{GPP + F_{in}}.$$
(S5)

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 CO₂ 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 CO₂ 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 CO₂ (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 (\sim 0.1-1 L), but averaged spatially to have representative values for the water body under investigation, or by eddy covariance (over spatial scales \sim 100-1000 m) (Berg et al., 2003). Respiration is calculated from oxygen consumption at night, which is then used to correct the douting not ovugan production to estimate gross primary productivity. Moreover, as for terrestrial

- 165 correct the daytime net oxygen production to estimate gross primary productivity. Moreover, as for terrestrial ecosystems, this approach neglects allochthonous CO₂ 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 ^{R_h}/_{GPP} in Eq. (S4)), leading to negative values of CUE_{ecosystem}, despite all organisms having positive CUE values. When accounting for C transport in and out of a heterotrophic system (Eq. (S5)), 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. (S5). As a result, $CSE_{ecosystem} > CUE_{ecosystem}$, although $CSE_{ecosystem}$ remains negative as long as the ecosystem is a net source of C.
- 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 ²³⁴Th flux-based measurements (Boyd and Trull, 2007; Giering et al., 2017; Le Moigne et al., 2015). This efficiency increases when less C is remineralized 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

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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_{eccosystem} in Eq. (S4)),

$$CSE_{watershed} = \frac{NECB}{GPP} = 1 - \frac{R + F_{out}}{GPP} = CUE_{ecosystem} - \frac{F_{out}}{GPP},$$
(S6)

where the net ecosystem carbon balance is evaluated in the whole watershed. Eq. (S6) 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.,

205 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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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	-
С	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
Fout	Abiotic carbon output	M L ⁻² T ⁻¹
GGE	Gross growth efficiency	-
GPP	Gross primary productivity	M L ⁻² T ⁻¹
Ι	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
0	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
<i>R_{maintenance}</i>	Maintenance respiration	M L ⁻² T ⁻¹ or M T ⁻¹
Roverflow	Overflow respiration	M L ⁻² T ⁻¹ or M T ⁻¹
R _{photo}	Photorespiration	M L ⁻² T ⁻¹
Т	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.

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/article s/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/ORN LDAAC/949)

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

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

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

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

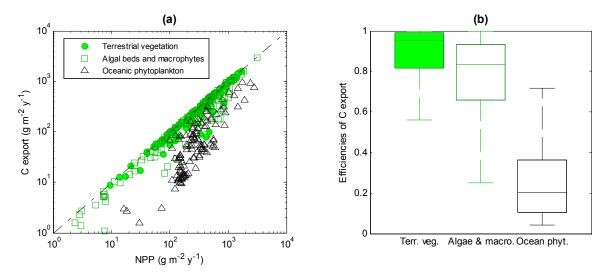




Figure S1. Comparison of the efficiencies of C export (exported C/primary production) among terrestrial and aquatic ecosystems. (a) Relation between C export rate and net primary productivity; (b) box plot of C-export efficiencies across ecosystem types. Data for terrestrial vegetation and algal beds/macrophytes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