

Individuals scale up carbon flow in ecosystems

Just Cebrían^{a,b,1}

^aDauphin Island Sea Lab, Dauphin Island, AL 36528; and ^bDepartment of Marine Sciences, University of South Alabama, Mobile, AL 36688

The distribution of energy and matter in ecosystems, as well as the rules that govern their flux and recycling rates, has received and continues to receive much attention (1). This is because elucidating the nature and controls of the flow and storage of elements such as carbon (C) and nitrogen (N) determines our understanding of services provided by ecosystems, such as the creation of food, C sequestration and buffering of climate change, and reduction of environmental pollution (2, 3). This elucidation is also important for our ability to understand and manage human impacts on the well-being of our planet (4). Many accounts of ecosystem elemental budgets now exist, particularly of C and N, and several attempts have been made to understand these budgets. Ecosystem-level processes, such as top-down control of elemental storage and recycling

rates by consumers (5), bottom-up uptake and storage regulation by nutrient availability (6), and multiple complex interactions, including the interplay of climate-forcing with the two former processes (7), have been invoked as determinants of matter and energy distribution in ecosystems. In PNAS, Schramski et al. (8) add yet another mechanism to the debate by providing evidence that the metabolic rates of the individual primary producers that compose the ecosystem control the rates of C accumulation and recycling in ecosystems.

Individual metabolic rates are at the heart of the metabolic theory of ecology (MTE). The central tenet of MTE is that organismal metabolic rates control the biological and ecological processes of the organisms. In turn, organismal metabolic rates are intimately associated to the body size and internal

temperature of the organism (9). By extension, it therefore follows that organismal body size and internal temperature can explain salient biological and ecological features of the systems the organisms compose. Using this foundation, MTE has made important strides in the last decade toward improving our understanding of the natural world, including organismal elemental content (10), development and productivity (11), speciation and distribution (12), and diversity (13). Because body size and temperature control organismal growth, they should also control the uptake and storage of elements, such as C, by organisms. Previous work has pointed out the potential of MTE to explain C cycling and storage in ecosystems (14), and now Schramski et al. (8) offer solid evidence to this effect.

For many decades ecologists have noted vast differences in the amount of C accumulated in ecosystems. Such differences apply to both terrestrial and aquatic ecosystems. Forests typically accumulate more C than grasslands, and beds of aquatic macrophytes, such as seagrass beds, accumulate more C than pelagic communities. Ecologists have also established that the rates at which C flows and recycles through the ecosystem are associated with C storage, with lower storage corresponding with faster recycling rates and lower C residence times (15). Schramski et al. (8) show that these trends are associated with the body size and internal temperature of the primary producers in the ecosystem.

The mechanism at the base of this association resides in the well-known dependence of organismal metabolic rate on body size and temperature (9). Such dependence implies that ecosystem gross primary production (i.e., C uptake by the ecosystem) is a function of the size (biomass) and internal temperature of all producers in the ecosystem (Fig. 1). Importantly, the dependence of gross primary production on producer size

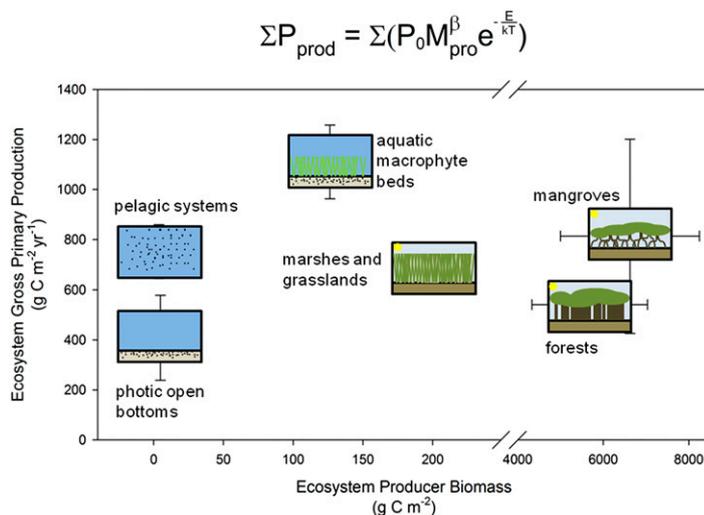


Fig. 1. The relationship between gross primary production (GPP, in $\text{g C m}^{-2} \text{ yr}^{-1}$) and producer biomass (PB, in g C m^{-2}) across aquatic and terrestrial systems. Note the overlap in GPP among systems, despite the large differences in PB. For systems composed of higher plants (all except pelagic systems and photic open bottoms), PB corresponds to the aboveground compartment. Mean values (\pm SE) are: pelagic systems: PB = $3.7 (\pm 0.6) \text{ g C m}^{-2}$; GPP = $752.2 (\pm 107.1) \text{ g C m}^{-2} \text{ yr}^{-1}$; photic open bottoms: PB = $4.8 (\pm 2.4) \text{ g C m}^{-2}$; GPP = $408.3 (\pm 170.1) \text{ g C m}^{-2} \text{ yr}^{-1}$; aquatic macrophyte beds: PB = $126.4 (\pm 19.1) \text{ g C m}^{-2}$; GPP = $1110.5 (\pm 147.5) \text{ g C m}^{-2} \text{ yr}^{-1}$; marshes and grasslands: PB = $201.2 (\pm 19.0) \text{ g C m}^{-2}$; GPP = $691.5 (\pm 97.4) \text{ g C m}^{-2} \text{ yr}^{-1}$; forests: PB = $5684.5 (\pm 1352.5) \text{ g C m}^{-2}$; GPP = $540.9 (\pm 56.0) \text{ g C m}^{-2} \text{ yr}^{-1}$; and mangroves: PB = $6625.1 (\pm 1622.6) \text{ g C m}^{-2}$; GPP = $813.8 (\pm 387.8) \text{ g C m}^{-2} \text{ yr}^{-1}$. Bars around the mean values correspond to the SE. The equation relating GPP (P_{prod}) to PB (M_{prod}) (see Eq. 5 in ref. 8) is on top of the figure.

Author contributions: J.C. designed research, performed research, contributed new reagents/analytic tools, analyzed data, and wrote the paper.

The author declares no conflict of interest.

See companion article 10.1073/pnas.1423502112.

¹Email: jcebrían@disl.org.

(biomass) is not linear, with gross primary production increasing proportionally less as producer biomass increases (the coefficient β is ~ 0.75) (9). The major finding by Schramski et al. (8) is that, when the effect of internal temperature is factored in along with the nonlinear dependence on producer biomass, we obtain similar levels of gross primary production across aquatic and terrestrial ecosystems (Fig. 1). Interestingly, this is the case despite the several orders-of-magnitude-wide differences in organismal size, and thus total biomass, found consistently across the ecosystems. Ecosystems composed of lignin-rich, larger producers (such as forests) have much higher levels of biomass, and thus C storage, than ecosystems composed of lignin-poor, smaller producers (such as pelagic systems). However, lignin-rich and lignin-poor ecosystems reach similar levels of gross primary production and, as a consequence, lignin-poor ecosystems feature faster C recycling rates and lower C residence times. MTE predicts accurately the several order-of-magnitude-wide differences in C recycling rates and residence time among ecosystems.

The association between C storage and residence time, on the one hand, and producer size (biomass), on the other hand, documented by Schramski et al. (8), is congruent with evidence provided by a number of cross-system comparisons. It has been long-established that C turns over more quickly in ecosystems composed of small producers (e.g., smaller producer biomass) in comparison with ecosystems composed of large producers (i.e., larger producer biomass; see ref. 16). Mechanistic manipulations with tracers also show that C cycles more quickly through the system, from uptake to producers to release back in the environment through respiration, in ecosystems composed of small producers (17, 18). Although these empirical results are robust, explanations of the specific mechanisms at their root have been elusive. The paper by Schramski et al. (8) sheds much welcome light by showing it is all a matter of underlying physiological principles

determining how much organisms can grow, or in this particular case take up C, given their body size and temperature. Because of the effects of body size and temperature on C uptake rates, smaller producers “rise to the bar” of gross primary production held by larger producers.

Previous work has pointed out the potential of MTE to explain C cycling and storage in ecosystems, and now Schramski et al. offer solid evidence to this effect.

The results of Schramski et al. (8) and congruent studies imply a number of important corollaries to further our understanding of C storage and flow in ecosystems. For example, similar levels of gross primary production, despite the contrastingly different levels of C storage across ecosystems, imply that ecosystems composed of smaller producers

sustain higher losses of producer biomass. Accordingly, higher mortality rates of producers (both through predation and natural senescence) have been reported for smaller-producer than larger-producer ecosystems (19, 20). MTE appears to be particularly well positioned to further explore these empirical relationships and improve our understanding of the mechanistic principles behind higher mortality rates in ecosystems with smaller producers. A codependent process may be the higher internal nutrient concentrations that are typically found in smaller producers, which may increase predation rates by herbivores, a process on which MTE has also provided some understanding recently (10, 14). Finally, through its importance for gross primary production, MTE also has the potential to illuminate many poorly understood aspects of ecosystem trophic dynamics. The future for MTE is certainly exciting. So long as the processes governing individual metabolism are scaled up to successfully explain ecosystem dynamics, MTE will undoubtedly become a powerful cornerstone to understand, predict, and manage current and future ecosystems.

- 1 Schmitz OJ, et al. (2013) Animating the carbon cycle. *Ecosystems* (N Y) 17(2):344–359.
- 2 Pauly D, et al. (2002) Towards sustainability in world fisheries. *Nature* 418(6898):689–695.
- 3 Cebrian J, et al. (2009) Producer nutritional quality controls ecosystem trophic structure. *PLoS ONE* 4(3):e4929.
- 4 Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277(5325):494–499.
- 5 Hairston NG, Jr, Hairston NG, Sr (1993) Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am Nat* 142(3):379–411.
- 6 Reich PB, et al. (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440(7086):922–925.
- 7 Elser JJ, et al. (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408(6812):578–580.
- 8 Schramski JR, Dell AI, Grady JM, Sibily RM, Brown JH (2015) Metabolic theory predicts whole-ecosystem properties. *Proc Natl Acad Sci USA*, 10.1073/pnas.1423502112.
- 9 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85(7):1771–1789.
- 10 Gillooly JF, et al. (2005) The metabolic basis of whole-organism RNA and phosphorus content. *Proc Natl Acad Sci USA* 102(33):11923–11927.
- 11 Savage VM, Gillooly JF, Brown JH, Charnov EL, Charnov EL (2004) Effects of body size and temperature on population growth. *Am Nat* 163(3):429–441.

- 12 Allen AP, Gillooly JF, Savage VM, Brown JH (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc Natl Acad Sci USA* 103(24):9130–9135.
- 13 Gillooly JF, Allen AP (2007) Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology* 88(8):1890–1894.
- 14 Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. *Funct Ecol* 19(2):202–213.
- 15 Cebrian J, Duarte CM (1995) Plant growth-rate dependence of detrital carbon storage in ecosystems. *Science* 268(5217):1606–1608.
- 16 Ricklefs RE (2007) *The Economy of Nature* (WH Freeman and Company, New York), p 550.
- 17 Pace ML, et al. (2004) Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427(6971):240–243.
- 18 Tobias CR, et al. (2003) Processing watershed-derived nitrogen in a well-flushed New England estuary. *Limnol Oceanogr* 48(5):1766–1778.
- 19 Cebrian J, Lartigue J (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecol Monogr* 74(2):237–259.
- 20 Marbà N, Duarte CM, Agustí S (2007) Allometric scaling of plant life history. *Proc Natl Acad Sci USA* 104(40):15777–15780.