

5. Natali, S. M. *et al.* *Glob. Change Biol.* **17**, 1394–1407 (2011).
 6. Dutta, K., Schuur, E. A. G., Neff, J. C. & Zimov, S. A. *Glob. Change Biol.* **12**, 2336–2351 (2006).
 7. Schuur, E. A. G. *et al.* *Nature* **459**, 556–559 (2009).
 8. Camill, P., Lynch, J. A., Clark, J. S., Adams, J. B. & Jordan, B. *Ecosystems* **4**, 461–478 (2001).
 9. Wickland, K.P., Striegl, R.G., Neff, J.C., Sachs, T. *J. Geophys. Res. Biogeosci.* **111**, G02011 (2006).
 10. Mikan, C. J., Schimel, J. P. & Doyle, A. P. *Soil Biol. Biochem.* **34**, 1785–1795 (2002).
 11. Johansson, T. *et al.* *Glob. Change Biol.* **12**, 2352–2369 (2006).
 12. Jorgenson M. T. *et al.* *Can. J. Forest Res.* **40**, 1219–1236 (2010).
 13. Lee, H., Schuur, E. A. G., Inglett, K. S., Lavoie, M & Chanton, J. P. *Glob. Change Biol.* **18**, 515–527 (2012).
 14. Sinsabaugh, R. L., Moorhead, D. L. & Linkins, A. E. *Appl. Soil Ecol.* **1**, 97–111 (1994).
 15. Prater, J. L., Chanton, J. P. & Whiting, G. J. *Glob. Biogeochem. Cycles* **21**, GB4004 (2007).

SOIL CARBON

Microbes and global carbon

The amount of organic material that microbes assimilate into their biomass is critical in regulating whether soils, the planet's main pool of organic matter, will absorb or emit carbon in a warmer world.

Joshua Schimel

The Earth system is, to a large extent, a product of microbial activity, yet microbial physiology is almost invisible in computer simulations of the Earth System. Would these models be improved if they treated decomposition as a by-product of microbial growth? Would this improve our ability to predict the planet's carbon cycle and its impact on the climate? Now, writing in *Nature Climate Change*, Wieder *et al.*¹ pose, and attempt to answer these questions.

For most of the Earth's history, the only organisms present were microorganisms (bacteria, fungi and algae). Even now they continue to have a dominant role in the cycling of chemicals around the Earth — the only biogeochemical process carried out predominantly by macroorganisms is photosynthesis. Because plants account for roughly 60% of global primary production, Earth system models (ESMs) increasingly use mechanistic approaches to predict how plant carbon uptake responds to environmental stressors and climate change by explicitly simulating plant physiological processes². So why have we not taken a similar approach to microbial processes?

Well, microbial physiology is not absent from ESMs — rather it is an implicit part of their formulation³. In ESMs, microbial processes such as decomposition and CO₂ release to the atmosphere are described with first order kinetics (chemical reaction rate) equations. In these, rates are dependent on the size of the substrate pool (the amount of organic carbon present), but are reduced when temperature or moisture are constraining:

$$dC/dt = -k C f_{\text{Temp}} f_{\text{Moisture}}$$

Here C is the size of the substrate pool, k is a rate constant that depends on the nature of the substrate and f is a functional response. There are no microbes visible in

this equation, but if there were no microbes present, the rate constant would be zero.

The microbiology is implicit and microbes' sensitivity to the environment is embedded

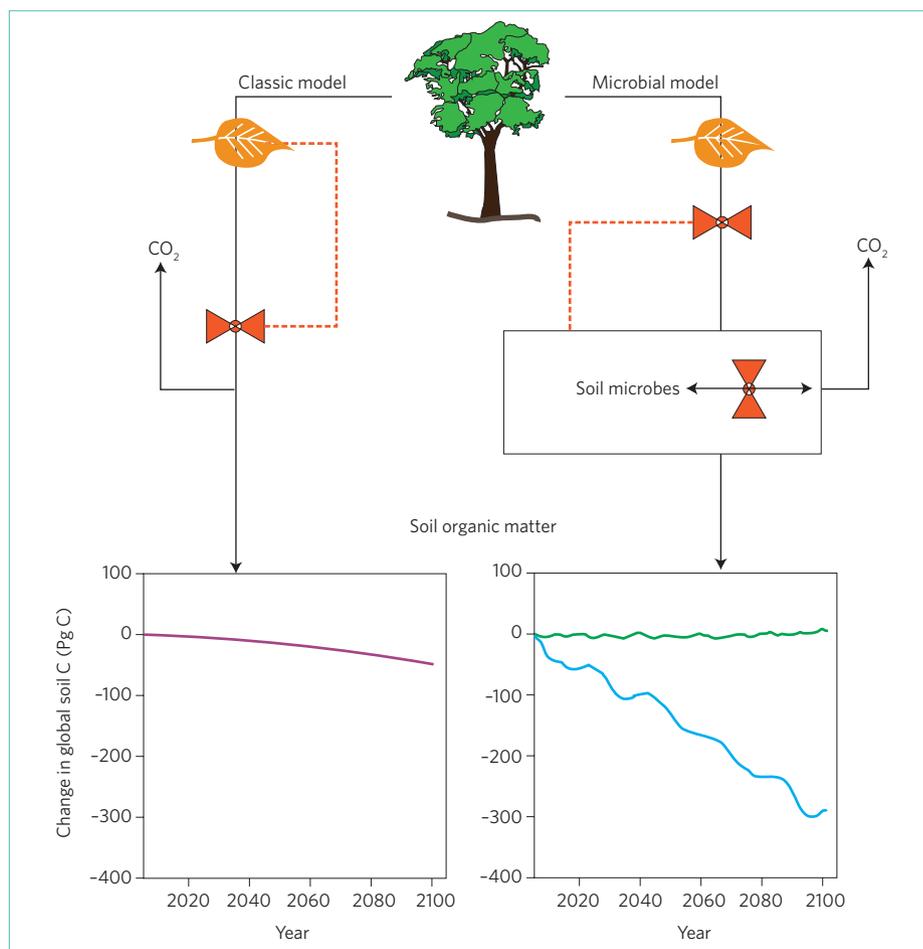


Figure 1 | The stabilization of plant carbon into soil carbon as represented in Earth system models. Left: A classical model, where decomposition is driven by substrate supply. Right: Model by Wieder *et al.* The size of the microbial community drives decomposition, whereas microbial growth efficiency regulates whether carbon is respired to CO₂ or is converted into microbial products. When MGE declines with temperature (green line), microbial biomass and decomposition decline, increasing soil C. When MGE is insensitive to temperature (blue line), biomass increases, accelerating decomposition and reducing soil C. Red symbols indicate major control mechanisms in the models.

in the response functions. Such models are based on the assumption that microbial communities remain in equilibrium with their environment and that their functional responses are stable. In other words, their response to temperature in a warmer future will be the same as today.

Implicit microbiology models are powerful and have the beauty of being both understandable and straightforward to parameterize. What we are less sure of is how accurate they are. Models use assumptions to process data so if those initial assumptions — the way the model 'thinks' — are wrong, so too will be the conclusions.

In their study, Wieder *et al.* challenged the assumption that the global carbon cycle and its response to warming can be accurately modelled using only first-order kinetics with implicit microbiology. The key issue they took on is that for plant litter to become stable soil carbon, microbes must not only break it down but must also resynthesize the carbon into new products. The proportion of the material that microbes assimilate, known as microbial growth efficiency (MGE), is central in this new model, as it controls decomposer populations and the proportion of carbon that is stabilized in the soil versus that lost to the atmosphere as CO₂.

They modelled decomposition as microbial physiology (Fig. 1), in which microorganisms decompose organic matter at a rate that follows Michaelis–Menten kinetics (a well-established model of enzyme reaction rates) and is proportional to their biomass, with each model parameter

sensitive to temperature. This included MGE; they tested whether its sensitivity to temperature would affect global carbon stores by incorporating this simple mechanistic formulation into a global-scale model (the Community Land Model) and compared it to a classic first-order implicit-microbiology model. This showed that the microbial model matched current global patterns of soil carbon better than did the classic approach.

Wieder *et al.* then tested how the different model versions respond to global warming, to investigate whether the global carbon cycle behaves differently when microbial physiology is accounted for. In the microbial model warming was found to accelerate microbial activity, but by reducing MGE it reduces microbial biomass and thus limits decomposition. This highlights MGE as perhaps the critical term in controlling the fate of soil carbon — if MGE is insensitive to temperature, warming will cause enormous carbon loss; if MGE declines with temperature, warming could even slightly increase global soil carbon (Fig. 1). As soils contain at least twice as much carbon in organic forms as is in the atmosphere as CO₂ (ref. 4), this distinction is important.

Understanding the physiology of microorganisms in soil is a challenge — a gram of soil typically houses 10,000 or more individual taxa living in the most physically complex habitat on Earth. Representing this complexity in a way that captures essential dynamics in a mathematically tractable form is a developing art. One of the key challenges is in deciding which are the essential processes to represent. Some models have

focused on the role of microbial extracellular enzymes⁵, others on mineral interactions⁶ and yet others on representing responses to pulse events⁷. The model by Wieder *et al.* highlights what may be the truly crucial question: when microbes take up an organic molecule, do they respire it — emitting it directly to the atmosphere — or do they resynthesize it into another organic form? If the latter, there is a chance that the carbon might be reformed into a molecule that gets trapped by soil minerals and sequestered; in which case increasing MGE would increase soil carbon. Alternatively, as assumed by Wieder *et al.*, it may become decomposer biomass, or enzymes that attack soil carbon. In this case, increasing MGE increases decomposition and reduces soil carbon. Which of these pathways dominates soil systems remains unclear, but as illustrated by Wieder *et al.*, it may be vital for the future of the Earth system. □

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References

1. Wieder, W. R., Bonan, G. B. & Allison, S. D. *Nature Clim. Change* **3**, 909–912 (2013).
2. Bonan, G. B., Oleson, K. W., Fisher, R. A., Lasslop, G. & Reichstein, M. *J. Geophys. Res.* **117**, G02026 (2012).
3. Schimel, J. P. in *Global Biogeochemical Cycles in the Climate System* (eds Schulze, E.-D. *et al.*) 177–183 (Academic, 2001).
4. Tarnocai, C. *et al. Glob. Biogeochem. Cycles* **23**, 1–11 (2009).
5. Moorhead, D. L., Lashermes, G. & Sinsabaugh, R. L. *Soil Biol. Biochem.* **53**, 133–141 (2012).
6. Koarashi, J., Hockaday, W. C., Masiello, C. A. & Trumbore, S. E. *J. Geophys. Res.* **117**, G03033 (2012).
7. Li, X. *et al. Geoderma* **159**, 440–451 (2010).