Conceptualizing biogeochemical reactions with an Ohm's law analogy

Jinyun Tang, William J. Riley, Gianna L. Maschmann, and Eoin L. Brodie

Earth and Environmental Sciences Area, Lawrence Berkeley National Laboratory, Berkeley, CA, 94720, USA

Corresponding author: J.Y. Tang (jinyuntang@lbl.gov)

Key Points:

- Ohm's law is proposed to formulate biogeochemical reactions.
- Ohm's law successfully models multiple substrates co-limited growth.
- Ohm's law may help building unified biogeochemical models.

Abstract: In studying problems like plant-soil-microbe interactions in environmental biogeochemistry and ecology, one usually has to quantify and model how substrates control the growth of, and interaction among, biological organisms. To address these substrate-consumer relationships, many substrate kinetics and growth rules have been developed, including the famous Monod kinetics for single substrate-based growth, Liebig's law of the minimum for multiple-nutrient co-limited growth, etc. However, the mechanistic basis that leads to these various concepts and mathematical formulations and the implications of their parameters are often quite uncertain. Here we show that an analogy based on Ohms' law in electric circuit theory is able to unify many of these different concepts and mathematical formulations. In this Ohm's law analogy, a resistor is defined by a combination of consumers' and substrates' kinetic traits. In particular, the resistance is equal to the mean first passage time that has been used by renewal theory to derive the Michaelis-Menten kinetics under substrate replete conditions for a single substrate as well as the predation rate of individual organisms. We further show that this analogy leads to important insights on various biogeochemical problems, such as (1) multiple-nutrient co-limited biological growth, (2) denitrification, (3) fermentation under aerobic conditions, (4) metabolic temperature sensitivity, and (5) the accuracy of Monod kinetics for describing bacterial growth. We expect our approach will help both modelers and non-modelers to better understand and formulate hypotheses when studying certain aspects of environmental biogeochemistry and ecology.

Plain Language Summary

Currently, scientists often use ad-hoc or empirical approaches to conceptualize and formulate biogeochemical processes encountered in environmental sciences. Here we propose that many biogeochemical processes can be coherently conceptualized and formulated using an analogy

based on the Ohm's law, a mathematical theory that is widely used to model electric circuits, and also the land-atmosphere exchange of water and energy. We show that this Ohm's law analogy is able to explain observations such as why microbial growth would follow the Monod kinetics, how sometimes fermentation could dominate aerobic respiration when glucose in great supply, how plant and microbes grow under multiple substrates co-limitation, etc. Since this Ohm's law analogy unifies the mathematical foundation of biogeophysics and biogeochemistry, we believe it can potentially lead to more robust land ecosystem models for projecting the climate change.

1. Introduction

In earth system modeling, biogeochemistry strongly affects mass and energy exchanges between ecosystems and the physical climate system [*Heinze et al.*, 2019]. Morphologically, biogeochemistry has three pillars: biology, geophysics, and chemistry. In the context of mathematical modeling, geophysics and chemistry generally have much stronger theoretical foundations than biology [*Brutsaert*, 2005; *Stumm and Morgan*, 1996; *Vallis*, 2006], even though all three are macroscale responses that emerge from atomic interactions, which in an ideal (but impractical) scenario can be predicted by solving the Schrödinger equation of all atoms together (so that arguably they all are subtopics of physics) [*Feynman et al.*, 2011b].

In seeking a better understanding of ecological dynamics, e.g., competition and symbiosis, mathematical formulations of the consumer-substrate relationship are essential for both theoretical modeling and interpreting empirical experiments [*Tilman*, 1982]. In the past, three approaches have been used to obtain such relationships. The first approach is by fitting certain empirical response functions to observational data [e.g., *Monod*, 1949]. The second approach is based on an ad-hoc heuristic conceptualization of the problem, e.g., the logistic equation was derived by adding a quadratic term to dissipate the exponential growth of a

population when Pierre-Francois Verhulst (1804-1849) was helping his teacher Alphonse Quetelet (1975-1874) to model human population dynamics [*Cramer*, 2002]. The third approach is based on systematic applications of some theory, such as the law of mass action [*Atkins et al.*, 2016], statistical mechanics [*Ma*, 1985], and renewal theory [*Doob*, 1948]. Notably, Michaelis-Menten kinetics (and some of its extensions) can be derived by applying any of these theories (see reviews in [*Kooijman*, 1998; *Swenson and Stadie*, 2019; *Tang and Riley*, 2013; 2017]), with the renewal theory even being able to show that Michaelis-Menten kinetics is the statistical mean of the stochastic description of a single enzyme molecule processing the substrate molecules [*English et al.*, 2006; *Reuveni et al.*, 2014].

Compared to the empirically-based and ad-hoc approaches, which generally provide limited understanding of the processes implied by the parameters, theory-based approaches have the advantage of linking various related albeit fragmented knowledge (that is abstracted from a much wider range of observations compared to the limited amounts of observational data used by the empirically-based approaches), thereby enabling a deeper understanding of the processes and systems of interest. For instance, when law of mass action is used to derive the Michaelis-Menten kinetics, using the related theory of chemical reaction rates (e.g., Smoluchowski's diffusion model of chemical reaction [*von Smoluchowski*, 1917]), *Tang and Riley* [2019b] were able to upscale the microbially-enabled reactions from one permease to a single bacteria cell and then to a representative soil volume (~O(1 cm^3)), and used the results to explain why substrate affinity parameters are highly variable in soil. Additionally, the theory-based approach has been used to derive the temperature response function of microbial activity [*Ghosh and Dill*, 2010], and to explain why Michaelis-Menten kinetics are more appropriate for microbial uptake of

92 small molecules, while reverse Michaelis-Menten kinetics are more appropriate for enzyme
93 degradation of organic polymer particles [*Tang and Riley*, 2019a].

94 In this paper, we first introduce an analogy that uses the Ohms' law from electric circuit
95 theory to interpret the resource-consumer relationship. Similar analogies have been widely used
96 by land models to represent the physics of land-atmosphere exchanges of water, gases, and
97 energy [e.g., *Lawrence et al.*, 2019; *Riley et al.*, 2011; *Shuttleworth and Wallace*, 1985; *Wu et*
98 *al.*, 2009]. (So that in a certain sense, the Ohm's law is unifying all three aspects of
99 biogeochemistry into physics.) We then exploit this analogy to explain several interesting
100 biogeochemical phenomena that are observed in various context. We conclude the paper with
101 recommendations of other potential applications of this analogy.

102 Although the example problems below are solved with the Ohm's law analogy, we note
103 that they can all be solved using the more accurate Equilibrium Chemistry Approximation (ECA)
104 kinetics [*Tang and Riley*, 2013] or the synthesizing unit plus ECA (SUPECA) kinetics [*Tang and*
105 *Riley*, 2017]. However, the Ohms' law analogy proposed here is more intuitive and can provide
106 an alternative to the ECA and SUPECA kinetics in formulating biogeochemical models.

107 **2 Methods**

108 **2.1 A brief review of Ohm's law and circuit theory**

109 We below briefly review Ohm's law and the theory of series and parallel resistor circuits.
110 More detailed descriptions of circuit theory can be found in *Feynman et al.* [2011a].

111 Ohm's law describes the relationship between voltage (V), electric current (I), and
112 resistor (r):

$$I = \frac{V}{r}. \quad (1)$$

To simplify the presentation, we assume that all variables are properly defined with their international units.

For a series concatenation of resistors r_j, application of Ohm's law yields

$$I = \frac{V}{\sum_j r_j}. \tag{2}$$

For a parallel concatenation of resistors r_j, application of Ohm's law leads to

$$I = V\left(\sum_j \frac{1}{r_j}\right), \tag{3}$$

and the electric current through each resistor is

$$I_j = \frac{V}{r_j}. \tag{4}$$

From equations (3) and (4), we can further derive

$$\frac{I_j}{I} = \frac{1}{1+\left(\sum_{l\neq j}\frac{r_j}{r_l}\right)}, \tag{5}$$

which states that when all other resistors are fixed, the fraction of current through r_j increases with decreasing r_j. We will see later that this inference is very useful to explain shifts in metabolic pathways in biological organisms.

2.2. Michaelis-Menten kinetics interpreted with Ohm's law

Michaelis-Menten kinetics represents the single-enzyme catalyzed single-substrate reaction velocity v as

$$v = \frac{v_{max}ES}{K+S}, \tag{6}$$

where, in the original application by *Michaelis and Menten* [1913], v_{max} is the maximum specific hydrolysis rate enabled by the invertase and E, S, and K are enzyme concentration, substrate concentration, and half saturation coefficient, respectively. We note that, for enzymes, K also includes contributions from the dissociation process [e.g., *Briggs and Haldane*, 1925].

By defining $k_f = v_{max}/K$, equation (6) can be rewritten as

$$v = \frac{E}{\frac{1}{v_{max}} + \frac{K}{v_{max}S}} = \frac{E}{\frac{1}{v_{max}} + \frac{1}{k_f S}}. \quad (7)$$

We then note that equations (7) and (1) are of the same form. Therefore, for Michaelis-Menten kinetics, if we apply the Ohm's law analogy by regarding E as voltage and v as current, the corresponding resistance is

$$r = \frac{1}{v_{max}} + \frac{1}{k_f S} = r_E + r_S, \quad (8)$$

where r_E represents the resistance as an intrinsic property (i.e., a kinetic trait) of the enzyme, and r_S represents the resistance introduced by the effective substrate delivery rate towards the enzyme. Further, r_E and r_S are of the unit of time, where (in the renewal theory [e.g., *Kooijman*, 1998]) r_E is the mean time for the enzyme to convert the enzyme-bound substrate molecules into product molecules and r_S is the mean time for the substrate molecules to approach the enzyme molecule and form enzyme-substrate complexes. Together, r is the mean first passage time of the stochastic description of how a single enzyme catalyzes the degradation of the substrate molecules [e.g., *Kooijman*, 1998; *Ninio*, 1987; *Qian*, 2008]. In particular, in many reactions, k_f is approximately proportional to the substrate diffusivity [*Alberty and Hammes*, 1958; *Chou and Jiang*, 1974], such that $k_f S$ is the diffusive substrate flux sensed by enzyme molecules. We then observe that r_S increases with the decrease of diffusive substrate flux, which can result from lower substrate concentration, or lower diffusivity (due to tortuosity, adsorption, or lower moisture in porous media like soil).

That the resistance r in equation (8) is of the time unit has also motivated some researchers to apply the time budget idea to derive predator-prey relationships [e.g., *Holling*, 1959; *Murdoch*, 1973], where r_E is referred as the mean time spent on handling the prey, and r_S

is the mean time for the predator to encounter the prey. However, few studies have pointed out the linkage between the time-budget analysis and Ohm's law, except that, based on a suggestion by *Thomsen et al.* [1994], *Almeida et al.* [1997] made an analogy of the membrane electron-transport chain to an electric circuit, and successfully used it to model denitrification. Recently, this method has been used by *Domingo-Felez and Smets* [2020] to build the Activated Sludge Model-Electron Competition (ASM-EC) model, which demonstrated the efficacy of this analogy in constructing robust biogeochemical models. Further, we noticed that the molecular biology of membrane electron transport chains and redox reactions are quite similar to the working principles of chemical batteries [*Schmidt-Rohr*, 2018], thereby motivating us to explore more extensively the applicability of Ohm's law analogy below.

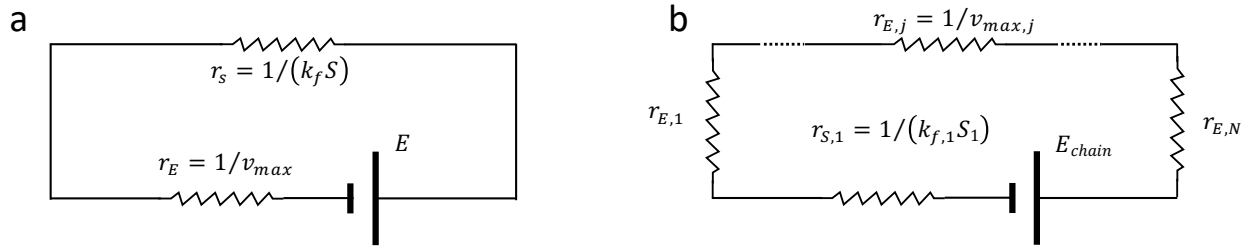


Figure 1**. a.** circuit schema for the Michaelis-Menten kinetics; **b**. series resistor-based schema for an enzyme chain and its reaction on substrate S_1, where dotted lines indicate multiple resistors $r_{E,j}$ concatenated in series. Symbols are explained in the main text**.**

In the Ohm's law analogy, kinetic interactions between an enzyme and its substrate molecules can be summarized as the battery-resistor relationship shown in Figure 1a, where the battery potential is enzyme concentration E, and the battery's resistance is r_E, while the appliance (i.e., substrate) has resistance r_S. However, we note that this analogy is accurate only when the substrate is non-limiting for the enzymes (i.e., when MM kinetics are more appropriate [*Tang and Riley*, 2019a]). For cases when substrate is limiting, the reverse Michaelis-Menten kinetics are more appropriate [*Tang*, 2015], and the roles of substrate and enzyme in the analogy

are reversed (such as for enzyme hydrolysis of polymeric organic matter; [*Tang and Riley*, 2019a]). (We note that the ECA kinetics are able to more accurately handle the wide range of substrate abundances with respect to enzymes [*Tang*, 2015].) We next show how the Ohm's law analogy will help us formulate biogeochemical kinetics for various situations.

3. Applications

3.1 Series resistor circuit-based formulation of chain-like enzyme reactions

Many metabolic pathways consist of a chain of reactions. Such examples include the Calvin-cycle (in photosynthesis), membrane electron transport chain, glycolysis, citric acid cycle, etc., and note that most of these reaction pathways involve cofactors [*Madigan et al.*, 2009; *Taiz and Zeiger*, 2006]. Nonetheless, assuming that at each step the enzyme and its co-factor together form an integrated enzyme unit to process the substrate delivered from a prior step, and the whole chain of enzymatic reactions are in detailed balance (i.e., the whole chain is in steady state without overflow [*Cao*, 2011], an assumption that is often made in flux balance models [*Orth et al.*, 2010]), we can then use the series circuit analogy to calculate the overall enzyme kinetics straightforwardly. According to the schema for this configuration (Figure 1b), when the whole enzyme chain is taken as a catalysis unit, the abundance of enzyme at the first step represents the voltage of the battery, and the total resistance is

$$r_{chain} = \left(\sum_{j=1}^{N} r_{E,j}\right) + r_{S,1} = r_E + r_{S,1}, \quad (9)$$

where $r_{E,j} = v_{max,j}^{-1}$ such that the first right hand side term is the total resistance represented by the maximum catalysis rate of the overall enzyme chain, and $r_{S,1} = \left(k_{f,1} S_1\right)^{-1}$ is the resistance due to the incoming substrate flux to the first enzyme in the chain. For the overall chain, the specific reaction rate for substrate processing is then

$$\frac{v_{chain}}{E_{chain}} = \frac{1}{r_{chain}} = \frac{\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)^{-1} S_1}{\frac{K_1}{v_{max,1}\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)} + S_1} \quad , \tag{10}$$

191 where $K_1 = v_{max,1}/k_{f,1}$. Equation (10) can be simplified as

$$\frac{v_{chain}}{E_{chain}} = \frac{v_{max,chain} S_1}{K_{chain} + S_1}, \tag{11}$$

192 with

$$v_{max,chain} = \left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)^{-1} < min_j\{v_{max,j}\}, \tag{12}$$

193 and

$$K_{chain} = \frac{K_1}{v_{max,1}\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)} = \frac{K_1}{1 + \sum_{j=2}^{N} v_{max,1}/v_{max,j}}. \tag{13}$$

194 From equation (10), we assert that an enzyme chain is equivalent to an enzyme unit with kinetic
195 traits $v_{max,chain}$ and K_{chain}. Moreover, from equations (12) and (13), we infer that increasing the
196 chain length decreases the overall reaction rate $v_{max,chain}$ (which is even slower than the
197 slowest step) and the half saturation coefficient K_{chain} of the enzyme chain.

198 Several interesting inferences can be additionally drawn from equations (9)-(13). First,
199 the second law of thermodynamics suggests that a thermal engine has higher thermodynamic
200 efficiency when it runs slower (and the highest efficiency can only be achieved when the system
201 is in thermodynamic equilibrium, i.e., not running at all [*Salamon et al.*, 2001]). Since a longer
202 reaction chain slows down the overall transformation rate from a given substrate to its final
203 product, (as an example,) application of the above equations to electron transport chains leads us
204 to assert that a longer chain will likely be thermodynamically more efficient (this argument
205 echoes the Ladder theorem in finite time thermodynamics; [*Salamon et al.*, 2017]). In contrast,
206 shorter electron transport chains imply faster use of substrates even though they result in less
207 efficient substrate use. Therefore, the length of electron transport chains can characterize the

tradeoff between substrate use rate and substrate use efficiency, an important selection factor for organisms during their evolution. Indeed, in one chemostat based study, *Chen et al.* [2017] found that Vibrionales bypass respiratory complex III to consume part of the oxygen using a cytochrome bd terminal oxidase to speed up growth, but the bioenergetic efficiency becomes ~32% as compared to ~80% for the longer canonical respiratory chain. Similarly, observations indicate that the less efficient fermentation pathway which has fewer enzymes involved is faster than the aerobic respiration pathway that has many more enzymes involved (thus is longer and more efficient; [*Madigan et al.*, 2009]). We will later (in section 3.5) use the parallel circuit analogy to explain why such bypassing of more efficient pathways will occur under substrate abundant conditions.

The second inference to be made is about the temperature sensitivity of parameters $v_{max,chain}$ and K_{chain}. In the simplest one-step case, $v_{max,chain}$ equals $v_{max,1}$, and K_{chain} equals K_1. According to transition state theory [e.g., *Eyring*, 1935], $v_{max,1}$ would have the following temperature dependence,

$$v_{max,1} = v_{max,1,ref} T \cdot exp\left(-\frac{\Delta G_1}{RT}\right), \tag{14}$$

where $v_{max,1,ref}$ is some reference reaction rate, T is temperature, ΔG_1 is the Gibbs energy of activation, and R is the universal gas constant. Similarly, for a reaction pathway consisting of a chain of enzymes, each $v_{max,j}$ will have a temperature dependence similar to that in equation (14), that is

$$v_{max,j} = v_{max,j,ref} T \cdot exp\left(-\frac{\Delta G_j}{RT}\right), \tag{15}$$

which when entered into equation (12), $v_{max,chain}$ will then be of the form

$$v_{max,chain} = \left[\sum_{j=1}^{N}\left(v_{max,j,ref}^{-1} exp\left(\frac{\Delta G_j - \Delta G_1}{RT}\right)\right)\right]^{-1} T \cdot exp\left(-\frac{\Delta G_1}{RT}\right). \tag{16}$$

Therefore, if $(\Delta G_j - \Delta G_1)/(RT) \ll 1$, the temperature dependence of $v_{max,chain}$ will be approximately like that in equation (14).

The temperature dependence of K_1 is determined by the temperature dependencies of $v_{max,1}$ and $k_{f,1}$. Inside the microbial cytoplasm and cell membrane (and also for whole microbial cells in most natural environments), $k_{f,1}$ is closely related to diffusivity [*Madigan et al.*, 2009]. Thus, according to the Stokes-Einstein equation of diffusivity ($D = (k_B T)/(6\pi\eta a)$, where k_B is the Boltzmann constant, η is the dynamic viscosity, and a is the radius of the spherical particle) [*Feynman et al.*, 2011c], $k_{f,1}$ can be approximated with a linear dependence on temperature divided by the temperature sensitivity of η (which is $exp(B/(T - T_{VF}))$, where B and T_{VF} are empirical parameters, according to the semi-empirical Vogel-Fulcher-Tamman-Hesse equation [*Garcia-Colin et al.*, 1989]). When the temperature dependence of $k_{f,1}$ is combined with the Eyring-type temperature dependence of $v_{max,1}$, the definition of K_1 ($= v_{max,1}/k_{f,1}$) suggests that its temperature dependence is of the Arrhenius type (because $exp(B/(T - T_{VF}))$ of the viscosity is very similar to the Arrhenius equation, and the linear temperature dependence of $k_{f,1}$ cancels out the linear part of the temperature dependence of $v_{max,1}$). Once again, if $(\Delta G_j - \Delta G_1)/(RT) \ll 1$, K_{chain} will probably have an Arrhenius-type temperature sensitivity as well.

When the above inferences are put into equation (11), we can then infer the temperature dependence of v_{chain}. From chemical thermodynamics, the temperature dependence of v_{chain} depends on chemical kinetics (as characterized by the Michaelis-Menten term, i.e., $\frac{v_{max,chain} S_1}{K_{chain} + S_1}$ in this example) and thermodynamics (as a function of the Gibbs free energy) of the enzyme catalyzed reaction. However, because enzymes are proteins, their conformational states are also

temperature dependent [*Murphy et al.*, 1990]. Thermodynamically, the undenatured (aka catalytically active) fraction of an enzyme population of length n_x (as measured by the number of amino acid residues) can be described as [*Murphy et al.*, 1990]

$$f_{ax} = \frac{1}{1+exp\left(-\frac{n_x \Delta G_x}{RT}\right)}, \quad (17)$$

where

$$\Delta G_x = \Delta H^* - T\Delta S^* + \Delta C_p[(T - T_H^*) - Tln(T/T_S^*)], \quad (18)$$

and

$$\Delta C_p = -46.0 + 30(1 - 1.54{n_x}^{-0.268})N_{CH,x}, \quad (19)$$

with heat capacity ΔC_P defined as the energy required to reorganize the water molecules surrounding the protein [*Ratkowsky et al.*, 2005]. ΔC_P increases with the non-polar accessible area of the molecule, as measured by $N_{CH,x}$, the average number of non-polar hydrogen atoms per amino acid residue. ΔC_p also measures the hydrophobic contribution, with higher values implying higher hydrophobicity (and notice that greater $N_{CH,x}$ implies higher hydrophobicity). Other parameters include ΔS^* as the enthalpy change at T_S^* (the convergence temperature for entropy) and ΔH^* as the enthalpy change at T_H^* (the convergence temperature for enthalpy), which can be considered to be constant under environmental conditions [e.g., *Ratkowsky et al.*, 2005]. Assuming $N_{CH,x}$ and n_x can be obtained from proteomic data for each type of enzyme [e.g., *Sawle and Ghosh*, 2011], we can then calculate $f_{ax,j}$ for all enzymes involved in the chain. Therefore, putting together the kinetic, thermodynamic, and catalytically active enzyme fraction functions, we obtain

$$v_{chain} = \frac{v_{max,chain}S}{K_{chain}+S} F_T \prod_j f_{ax,j}, \quad (20)$$

where the thermodynamic temperature dependence of the reaction is

$$F_T = 1 - exp\left(-\frac{\Delta G_{reac}}{RT}\right), \quad (21)$$

with ΔG_{reac} being the Gibbs free energy of the overall reaction being catalyzed, which is defined by the chemical activity of initial substrates and final products [e.g., *Jin and Bethke*, 2007].

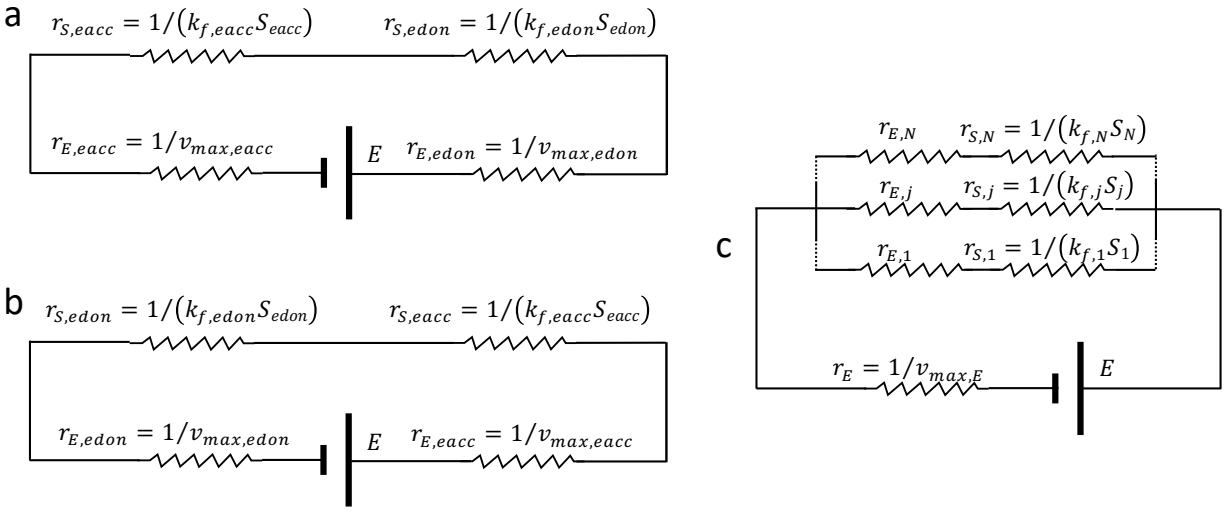


Figure 2. **a**. type-1 circuit schema for redox-type reaction; **b**. type-2 circuit schema for redox-type reaction; **c**. circuit schema for parallel resistor-based schema for competitive enzymatic reactions. Type-1 and Type-2 schema are equivalent, and are not differentiated in the Ohm's law analogy. Symbols are explained in the main text.

Unless equation (20) is applied to organisms capable of growing on alternative electron acceptors or donors, and the system is undergoing fast transition in redox status (e.g., at the depth of the soil water table), F_T is very close to 1, and can be ignored. Therefore, the temperature dependence of v_{chain} is dominated by the kinetic term (i.e., that of the Michaelis-Menten term) and the temperature dependent fraction of active enzymes ($\prod_j f_{ax,j}$). The kinetic term increases with temperature, while the fraction of active enzymes first increases, then decreases with temperature. The overall temperature sensitivity of the reaction chain will be of the form predicted by the macromolecular rate theory (MMRT) (with fine tuning from substrate availability through the kinetic term which MMRT does not consider) [*Arcus et al.*, 2016; *Schipper et al.*, 2014]. Therefore, for a population of cells that are not under substrate limitation

and steadily growing (so that one metabolic pathway dominates the metabolism), one should expect a MMRT type temperature dependence of the metabolic rates. This thus explains why *Ratkowsky et al.* [2005] was able to use the following equation to model bacterial growth rates under unlimited substrate supply:

$$g = \frac{cTexp(-\Delta H_A/RT)}{1+exp\left(-\frac{n}{RT}(\Delta H^* - T\Delta S^* + \Delta C_p[(T-T_H^*) - Tln(T/T_S^*)])\right)}, \quad (22)$$

where g is growth rate, c is an empirical constant, and ΔH_A is substrate dependent activation energy. However, unlike it was historically assumed that properties of some single control enzyme determine the overgrowth [*Johnson and Lewin*, 1946], here n and ΔC_p represent mean values of protein length and their thermal property, under possible influences from other molecules, such as phospholipids [e.g., *Mansy and Szostak*, 2008].

3.2 Series resistor-based formulation of enzyme catalyzed redox reactions

Many biogeochemical processes are of the redox type, including photosynthesis, aerobic respiration, nitrification, anaerobic denitrification, etc. [*Madigan et al.*, 2009; *Taiz and Zeiger*, 2006]. Basically, enzyme catalyzed redox reactions facilitate electron transfers from electron donors to electron acceptors. This process can be summarized with the schema Figure 2a that has one resistor representing electron donors ($r_{S,edon}$), and the other resistor ($r_{S,eacc}$) representing electron acceptors, with the enzyme being the battery. By applying the Ohm's law analogy, the reaction rate is

$$v = \frac{E}{r_{eacc}+r_{edon}}, \quad (23)$$

where $r_{eacc} = \frac{1}{v_{max,eacc}} + \frac{1}{k_{f,eacc}S_{eacc}}$, and $r_{e,acc} = \frac{1}{v_{max,edon}} + \frac{1}{k_{f,edon}S_{edon}}$. When the two are combined, equation (23) can be rewritten as

$$v = \frac{E}{r_E + \frac{1}{k_{f,eacc} S_{eacc}} + \frac{1}{k_{f,edon} S_{edon}}}. \quad (24)$$

with $r_E = \frac{1}{v_{max,eacc}} + \frac{1}{v_{max,edon}}$, $r_{S,eacc} = \frac{1}{k_{f,eacc} S_{eacc}}$, and $r_{S,edon} = \frac{1}{k_{f,edon} S_{edon}}$. We note that in this series resistor-based formulation, the total resistance (or mean first passage time) does not include the discount resulting from the concurrent binding of electron donors and acceptors to the enzyme (i.e., configuration Figure 2b is as good as Figure 2a, and they have the same resistance). However, this discount can be incorporated by renewal theory (or law of mass action), which leads to the synthesizing unit (SU) model [*Kooijman*, 1998] below

$$v = \frac{E}{r_E + \frac{1}{k_{f,eacc} S_{eacc}} + \frac{1}{k_{f,edon} S_{edon}} - \frac{1}{k_{f,eacc} S_{eacc} + k_{f,edon} S_{edon}}}. \quad (25)$$

Compared to equation (24), the SU model (i.e., equation (25)) is numerically more accurate (in approximating the law of mass action, the standard method that deals with biogeochemical reactions [*Koudriavstev et al.*, 2001]). Equations (24) and (25) differ by the additional term $-1/\left(k_{f,eacc} S_{eacc} + k_{f,edon} S_{edon}\right)$ that accounts for the co-existence of schemas in Figure 2a and Figure 2b.

Equation (24) was derived as early as in *Alberty* [1953], and is called the additive model. It was found as the superior formulation to model multiple nutrient limitations of microbial and plant growth in *O'Neill et al.* [1989] (where electron donors and acceptors are replaced with complementary nutrients, such as nitrogen and phosphorus). In particular, the additive model equation (24) can be extended to include arbitrary number of nutrients:

$$v = \frac{E}{r_E + \sum_j \frac{1}{k_{f,j} S_j}}. \quad (26)$$

where S_j can be essential nutrients including carbon, nitrogen, phosphorus, potassium, chloronium, etc. *Smith* [1976; 1979] used equation (26) to model plant growth and microbial

321 growth under carbon, nitrogen, phosphorus, and potassium co-limitation. Based on past
322 successful applications [*Franklin et al.*, 2011; *Kooijman*, 1998], the SU model (i.e., equation
323 (25)) may be argued as mathematically more rigorous than the series resistor-based additive
324 model (i.e., equation (24) or (26)). However, given the usually significant uncertainty of
325 ecological data, the series resistor-based additive model may be equally good. Indeed, when we
326 applied both the SU model and the resistor-based additive model to the measured algal growth
327 rates under various levels of phosphorus and vitamin B_{12} additions [*Droop*, 1974], both models
328 can be satisfyingly calibrated with respect to the growth data (Figure 3a and b). Further, when
329 the normalized growth rates are contoured as a function of the normalized substrate fluxes, the
330 SU and resistor-based additive models show very similar growth patterns (Figure 3c and d). The
331 SU model and additive model also performed equally well for the plant growth data from *Shaver*
332 *and Melillo* [1984] (Figure 4). Moreover, when the SU model and additive model are used to
333 model aerobic heterotrophic respiration using the parameterization from *Tang and Riley* [2019b],
334 we once again find the two models resulted in very similar goodness of fit with respect to the
335 measurements (Figure 5). These lines of evidence suggest that one can probably use these two
336 models alternatively. In particular, both can be a substitute for Liebig's law of the minimum that
337 is used by most existing biogeochemical models [*Achat et al.*, 2016].
338 Additionally, we note that equation (26) can be extended into a photosynthesis model to
339 replace the Farquhar or Collatz model that is formulated based on Liebig's law of the minimum,
340 which has to arbitrarily smooth the abrupt transitions from one limiting process to another [e.g.,
341 *Collatz et al.*, 1990; *Collatz et al.*, 1992; *Farquhar et al.*, 1980; *Kirschbaum and Farquhar*,
342 1984]. In this context, we contend that it is possible to use the same kinetics to formulate models

of plant photosynthesis, microbial substrate dynamics, and biomass growth, a strategy that will likely enhance the mathematical coherence in modeling plant-soil-microbial interactions.

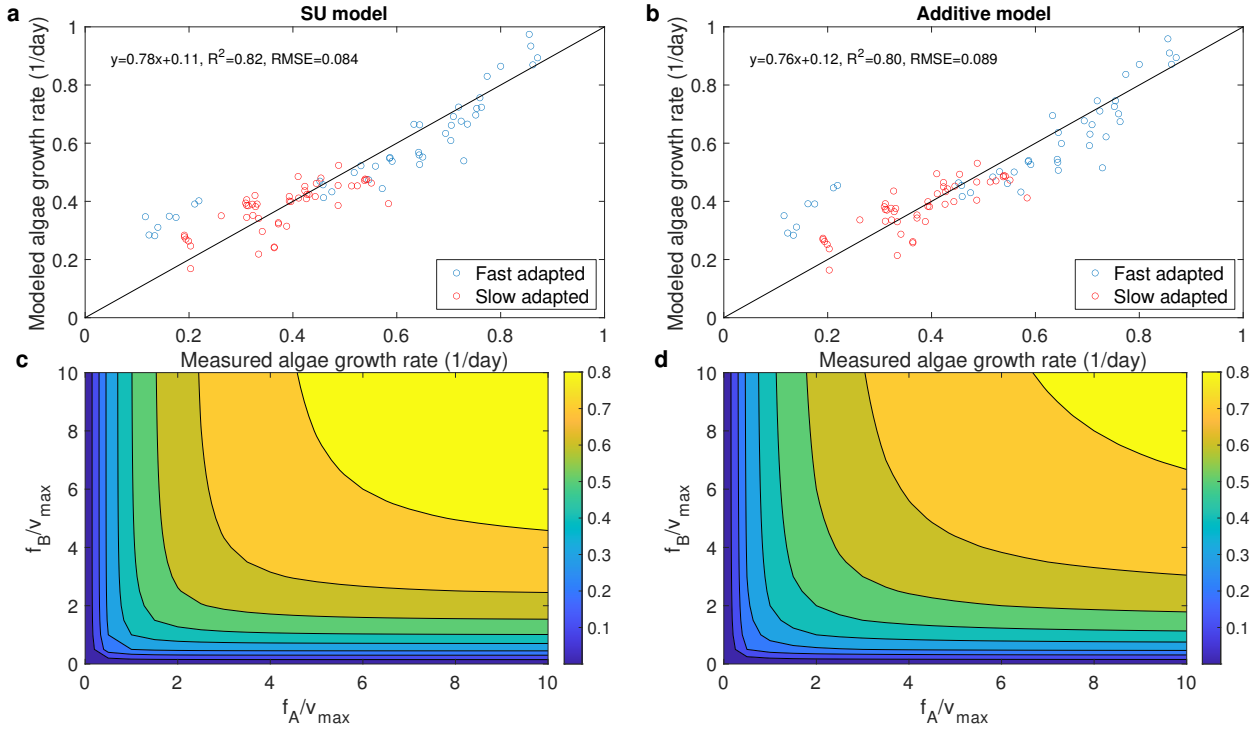


Figure 3 **a** comparison of the calibrated synthesizing unit (SU) model prediction for the algal growth rates data from *Droop* [1974]; **b** same as **a** but from the calibrated resistor-based additive model; **c** contour of normalized growth rate as a function of normalized fluxes of substrates A and B for the SU model; **d** same as **c** but for the resistor-based additive model. The additive model is presented as equation (24), and the SU model is presented as equation (25). Model parameters are in Table S1 of the supplemental material.

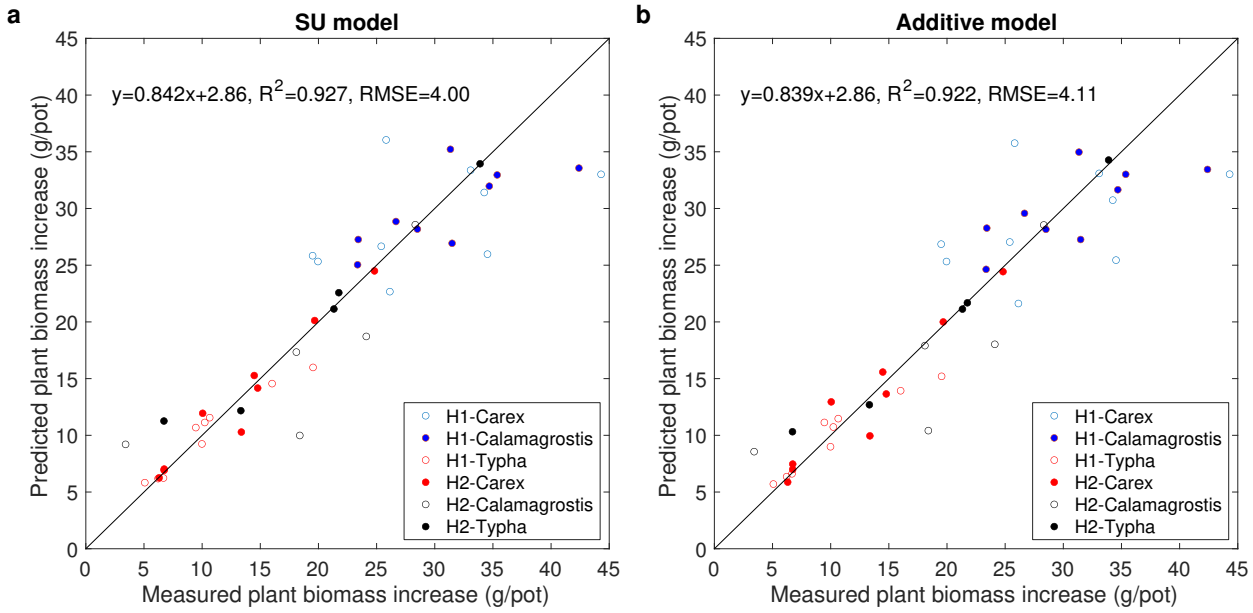


Figure 4 **a** SU model predicted vs measured plant growth; **b** Additive model predicted vs measured plant growth. The data is from *Shaver and Melillo* [1984]. Model parameters are in Table S1 of the supplemental material.

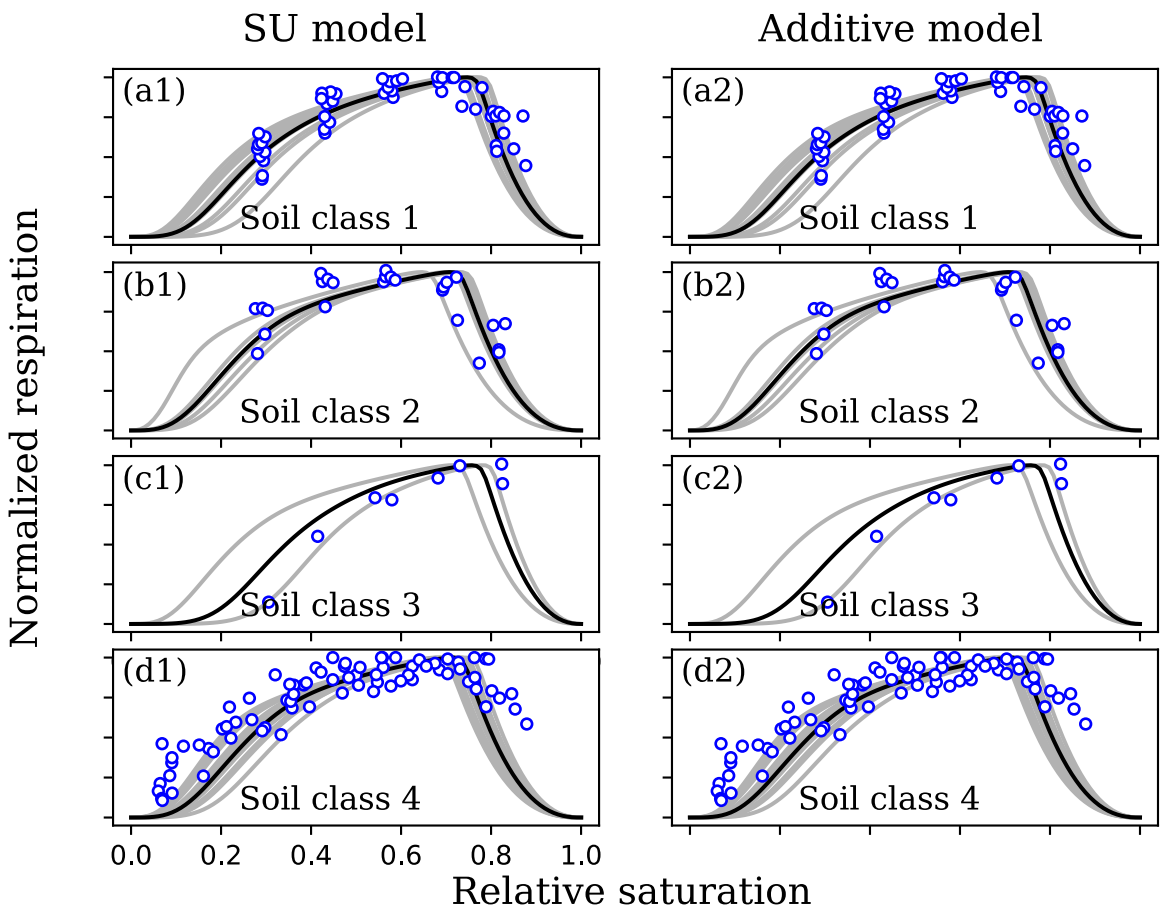
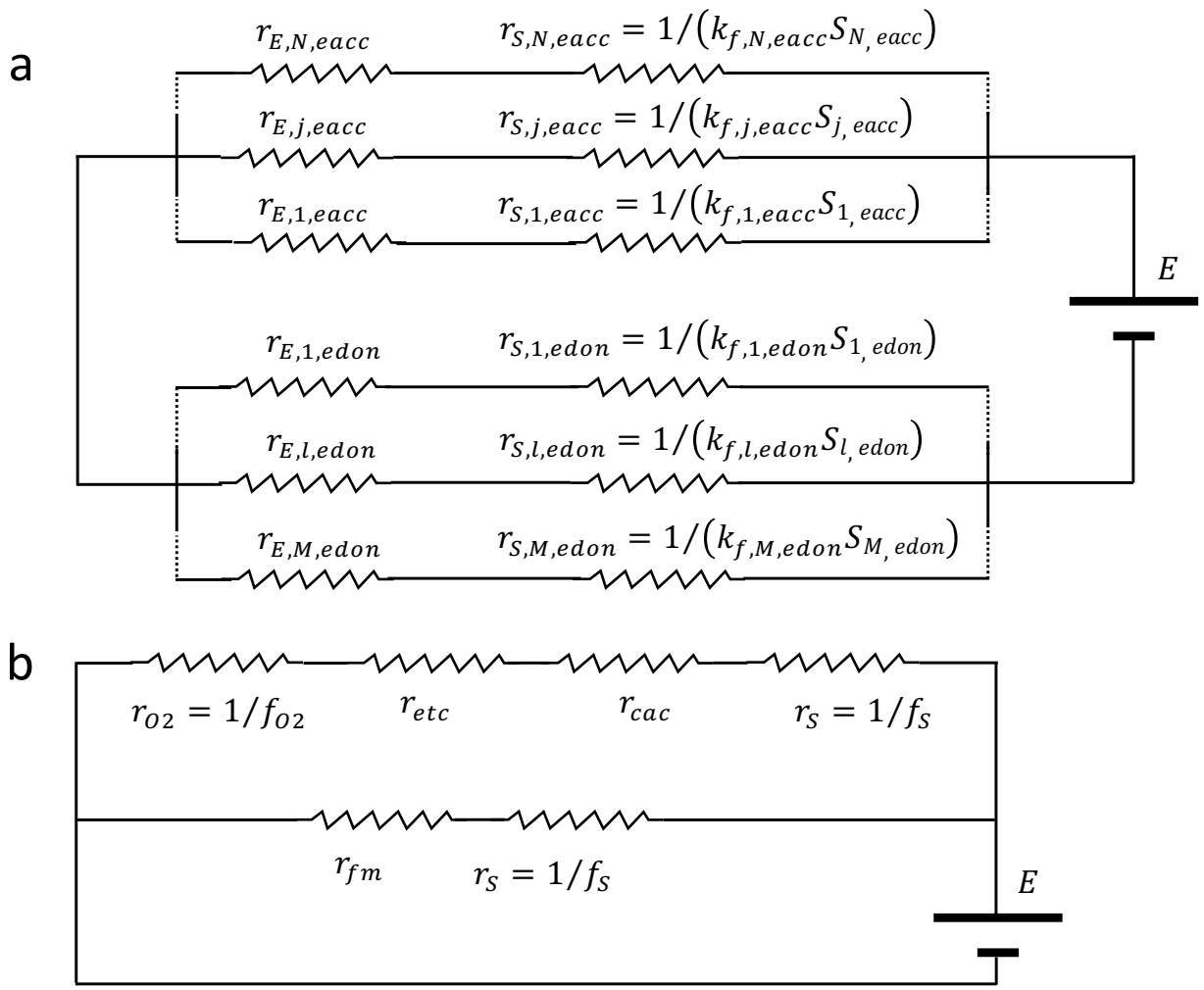


Figure 5. Left panels are SU model-based prediction of respiration-soil-moisture relationship; right panels are based on the resistor-based additive model. The two models used identical parameters, which are detailed in *Tang and Riley* [2019b]. The statistics for model-data fitting (in terms of linear regression and root mean square error) between two models are identical to 0.01 (see Table S2 of the supplemental material).

3.3 Parallel resistor-based formulation of competitive kinetics

Many microorganisms can feed on multiple substrates. For example, *E.coli* and yeasts are able to perform both aerobic and anaerobic respiration [e.g., *Dashko et al.*, 2014; *Unden and Bongaerts*, 1997]. Meanwhile, some enzymes can react on different substrates, e.g., enzyme ribonuclease is able to degrade various RNA molecules [*Etienne et al.*, 2020]. Thus, we next show that such problems can be formulated using the parallel circuit (plus one series resistor) analogy.



370

371 Figure 6. **a** mixed resistor circuit schema for redox reactions with alternative electron donors and
372 acceptors; **b** circuit schema for the parallel fermentation and aerobic respiration pathways.
373 Symbols are explained in the main text.

374 We first formulate the competitive Michaelis-Menten kinetics using the schema in Figure

375 2c. For this case, the total resistance is

$$r = r_E + r_S = r_E + \left(\sum_j \left(r_{E,j} + r_{S,j}\right)^{-1}\right)^{-1}, \tag{27}$$

376 where ${r_{S,j}}^{-1} = k_{f,j}S_j$, and $r_{E,j}$ is the resistance due to preprocessing of substrate S_j before it is

377 handed to the central enzyme E (i.e., the enzyme that products of all substrates have to pass

378 through), and $r_E = 1/v_{max,E}$ is the resistance due to the maximum substrate processing rate of

379 the central enzyme (which for redox-reactions could be determined by the time spent on
380 processing the electron donors if S_j here are electron acceptors). If $r_{E,j} = 0$, which is usually
381 assumed for competitive Michaelis-Menten kinetics, the second term r_S becomes $\left(\sum_j k_{f,j} S_j\right)^{-1}$,
382 and the reaction velocity is

$$v = \frac{E}{r} = \frac{E}{\frac{1}{v_{max}} + \left(\sum_j k_{f,j} S_j\right)^{-1}}, \tag{28}$$

383 and the corresponding flux through pathway j is

$$v_j = \frac{v r_S}{r_{S,j}} = v \frac{k_{f,j} S_j}{\sum_l k_{f,l} S_l} = E \cdot \frac{v_{max} S_j / K_j}{1 + \sum_l S_l / K_l}, \tag{29}$$

384 where $K_j = v_{max} / k_{f,j}$. It is easy to see that v_j is the reaction velocity computed from the
385 competitive Michaelis-Menten kinetics. We note that equation (29) is meaningful only when
386 pathway j produces new molecules. However, even for inhibitors, whose binding to enzymes
387 does not produce new molecules, if we regard dissociation as a way of producing new molecules,
388 then equation (29) is still mathematically meaningful.

389 **3.4 Mixed series and parallel resistor-based formulation of redox reactions of alternative**
390 **electron donors and acceptors**

391 Many microorganisms (such as denitrifying bacteria; e.g., *Robertson and Groffman*
392 [2015]) are able to grow on different electron donors and acceptors. Such problems can be solved
393 using the SUPECA kinetics [*Tang and Riley*, 2017]. Below we formulate it using the schema of
394 mixed series and parallel resistors.

395 Based on the schema in Figure 6a, the total resistance is

$$r = r_{edon} + r_{eacc} = \left(\sum_l {r_{l,edon}}^{-1}\right)^{-1} + \left(\sum_j {r_{j,eacc}}^{-1}\right)^{-1}, \tag{30}$$

396 where the resistance for electron donors is

$$r_{l,edon} = r_{E,l,eacc} + r_{S,l,eacc} = \frac{1}{v_{max,l,eacc}} + \frac{1}{k_{f,l} S_{l,eacc}}, \quad (31)$$

397 and the resistance for electron acceptors is

$$r_{j,eacc} = r_{E,j,edon} + r_{S,j,edon} = \frac{1}{v_{max,j,edon}} + \frac{1}{k_{f,j,edon} S_{j,edon}}. \quad (32)$$

398 Accordingly, the corresponding reaction flux through electron donor j is

$$v_{j,edon} = \frac{E}{r} \frac{r_{edon}}{r_{j,edon}} = \frac{E}{r_{j,edon}} \frac{r_{edon}}{r_{edon} + r_{eacc}}, \quad (33)$$

399 while the corresponding reaction flux through electron acceptor j is

$$v_{j,eacc} = \frac{E}{r} \frac{r_{eacc}}{r_{j,eacc}} = \frac{E}{r_{j,eacc}} \frac{r_{eacc}}{r_{edon} + r_{eacc}}. \quad (34)$$

400 Now considering an application that involves two electron acceptors, e.g., nitrate and nitrite in

401 denitrification, we have

$$\frac{1}{r_{eacc}} = \frac{1}{r_{NO3}} + \frac{1}{r_{NO2}}, \quad (35)$$

402 which when combined with equation (34) leads to

$$v_{NO3} = \frac{E}{r_{NO3} + r_{edon} + r_{edon} r_{NO3} / r_{NO2}}, \quad (36)$$

403 and

$$v_{NO2} = \frac{E}{r_{NO2} + r_{edon} + r_{edon} r_{NO2} / r_{NO3}}, \quad (37)$$

404 which are just the equations (10) in *Almeida et al.* [1997] that have been successfully used to fit

405 the measurement of denitrification rates from *Almeida et al.* [1995]. With proper number of

406 resistors, the denitrifier model by *Domingo-Felez and Smets* [2020] can also be easily recovered

407 from equations (30)-(34).

408 **3.5 Other potential applications of the Ohm's law analogy**

409 Besides the applications described above, we below use the Ohm's law analogy to derive

410 some quite interesting results.

First, we will explain why fermentation can occur even when there is still oxygen to support the energetically more efficient aerobic respiration. Such a phenomenon is called the Warburg effect (i.e., lactate producing aerobic fermentation) in proliferating mammalian cells (a phenomenon important to the understanding of cancer development), or the Crabtree effect (i.e., ethanol fermentation) of unicellular yeast Sacchamoyces cerevisiae [e.g., *de Alteriis et al.*, 2018]. *E. coli* have also been observed to shift to the seemingly less efficient yet faster metabolic pathways under high substrate concentrations [e.g., *Flamholz et al.*, 2013; *Labhsetwar et al.*, 2014]. Depending on the details to be represented, we acknowledge that there are multiple ways to model such phenomenon even with the circuit analogy. We next present one of these mathematical explanations to show that, under certain aerobic conditions, high glucose concentration makes fermentation more favorable.

According to the schema in Figure 6b, the specific ATP generation rate from the fermentation pathway is

$$v_{FM,ATP} = \frac{Y_{FM}}{\frac{1}{f_S}+r_{fm}}, \tag{38}$$

where f_S is the incoming flux of pyruvate (produced from glycolysis) sensed by the two metabolic pathways (which is proportional to the incoming glucose flux sensed by the organism under steady-state), r_{fm} is the resistance associated with the conversion of pyruvate into fermentation products (which could be lactate, ethanol, or acetate depending on the organism; [*Madigan et al.*, 2009]), and Y_{FM} is the ATP yield of fermentation. Similarly, the specific ATP generation rate from the aerobic respiration pathway is

$$v_{AO,ATP} = \frac{Y_{AO}}{\frac{1}{f_S}+r_{cac}+r_{etc}+\frac{1}{f_{O2}}}, \tag{39}$$

where r_{acc} and r_{etc} are resistance associated with the citric acid cycle, and the electron transport chain, respectively. f_{O2} is the incoming oxygen flux, and Y_{AO} is the ATP yield of aerobic respiration. Because the citric acid cycle involves many more enzyme-catalyzed steps than fermentation, $r_{cac} > r_{fm}$. Meanwhile, Y_{AO} is about 20 times the value of Y_{fm}[*Madigan et al.*, 2009].

In a metabolically active organism, for fermentation to be more favorable than aerobic respiration, the following condition needs to be satisfied,

$$\frac{Y_{FM}}{Y_{AO}} > \frac{\frac{1}{f_S}+r_{fm}}{\frac{1}{f_S}+r_{cac}+r_{etc}+\frac{1}{f_{O2}}} > \frac{r_{fm}}{r_{cac}+r_{etc}+\frac{1}{f_{O2}}}, \tag{40}$$

where the term after the second ">" suggests that fermentation is more favorable only when oxygen is below a certain level of availability (note that f_{O2} is approximately proportional to diffusion). When the oxygen availability is sufficiently low, higher substrate concentration (i.e., greater f_S) will make fermentation more effective in generating ATP. If we further consider that the fermentation pathway requires the organism to maintain a much smaller number of enzymes than required for the aerobic oxidation pathway (which is equivalent to increase the value of Y_{FM}/Y_{AO}, making the inequality (40) easier to be satisfied), we can expect fermentation to be preferred for high supply of glucose (i.e., greater f_S) even under certain aerobic conditions. (For anaerobic condition, f_{O2} approaches zero, and the inequality (40) is easily satisfied). Given the significance of this problem in various contexts, including methane and hydrogen dynamics in environment and industrial biogeochemistry [*Lu et al.*, 2009; *Madigan et al.*, 2009], we expect to study this problem in a more quantitative and extensive way elsewhere.

Another very interesting application is to qualitatively explain why Monod kinetics can fit the substrate-growth rate relationship of an exponentially growing bacterial population

[*Monod*, 1949]. The argument goes like the following. For an exponentially growing bacterial population, the bacteria proteomes are in steady state. Meanwhile, from the Ohm's law analogy described here, we know that any functioning circuit-network can be equivalently represented by a bulk resistor. Therefore, we contend that however complex the circuit representation of a bacterial metabolism would be, it as a whole can be equivalently represented by a resistor r_E. When this r_E is combined with the resistance associated with the incoming substrate flux (see equation (7)), we say that the bacterial growth would very likely follow the Monod kinetics. However, when the bacteria are in transition from one metabolic state into another, extra resistors are introduced accompanying the change of proteomes, and Monod kinetics will fail for such situations [e.g., *Erickson et al.*, 2017]. This argument also explains why models based on flux balance analysis with proteomic constraints can simulate steadily growing *E. coli* and yeast realistically [*Labhsetwar et al.*, 2014; *Labhsetwar et al.*, 2017].

3.6 Limitations of the Ohm's law analogy

While the Ohm's law analogy can be used to model many challenging biogeochemical processes, it is not appropriate for all types of networks. For instance, it is not able to properly couple two or more consumers (i.e., two or more batteries) within a single circuit network, even though the electric-circuit theory itself does not forbid such a configuration to occur (which can be solved with the Kirchhoff's law of voltage and current [e.g., *Feynman et al.*, 2011a]). Rather, such coupling can only be done by first representing the substrate dynamics of each consumer separately, and then coupling them together by differential equations. Such coupling could be critical when many consumers are competing for a limited substrate, even though none of the consumers is substrate-limited when other consumers are excluded [e.g., *Etienne et al.*, 2020]. The equilibrium chemistry approximation (ECA) kinetics [*Tang and Riley*, 2013] and its progeny

SUPECA kinetics [*Tang and Riley*, 2017] are more capable of resolving such situations. In soil biogeochemistry, one such situation is to model the interaction of a substrate molecule (e.g., ammonium, inorganic phosphorus, or dissolved organic carbon) that is simultaneously undergoing uptake by organisms and adsorption by mineral surfaces. Fortunately, a simple remedy is possible for the Ohm's law analogy from the ECA kinetics. In the ECA kinetics, microbial uptake of substrate S under the influence of adsorption by mineral surface M (with affinity parameter K_M) is

$$F = \frac{v_{max} SB}{K + S + MK/K_M + \alpha B}, \tag{41}$$

where K is the half saturation constant for the uptake of S by microbe B in the absence of M, and αB is the within-population competition effect introduced by ECA. *Tang and Riley* [2019a] showed that αB is negligible due to the large size contrast between microbes (and likewise fine roots) and substrate molecules. When αB is ignored, equation (41) becomes

$$F = \frac{B}{\frac{1}{v_{max}} + \frac{1}{k_f S}\left(1 + \frac{M}{K_M}\right)} = \frac{B}{\frac{1}{v_{max}} + \frac{1}{k_f^* S}}, \tag{42}$$

with

$$k_f^* = k_f \Big/ \left(1 + \frac{M}{K_M}\right). \tag{43}$$

Now the Ohm's law analogy will still work if $1/k_f^* S$ is used to defined the substrate dependent resistance. Moreover, equation (43) suggests that mineral surfaces may slow the microbial uptake of substrate S by effectively reducing the substrate delivery rate towards the microbes. However, when the sizes of substrates and competitors are similar (e.g., in some predator-prey relationships), the Ohm's law analogy will be too cumbersome to apply, and the ECA or SUPECA kinetics should be used. Nonetheless, it will be very interesting and helpful to

construct and compare models for the same system using both the Ohm's law analogy and ECA (or SUPECA) kinetics.

4 Conclusions

By applying the mathematical similarity between the Ohm's law and Michaelis-Menten kinetics, we show that the electric circuit analogy can be used to derive many interesting results of biogeochemical kinetics. We show this approach reproduces many successful applications in the literature, including aerobic heterotrophic respiration, multi-nutrient co-limited microbial (and plant) growth, denitrification dynamics, etc. This approach also sheds new insights on the Warburg and Crabtree effect in prokaryotes and eukaryotes, and conceptually explains why the Monod relationship accurately represents the kinetics of steadily-growing bacterial populations, and why flux balance modeling with proteomic constraints is able to accurately model microbial growth. Based on these results, we expect that the Ohm's law analogy will help build a unified kinetic modelling framework of microbial and plant biogeochemistry to make more robust predictions.

Data Availability Statement

Data is available through *Shaver and Melillo* [1984], *Droop* [1974], *Franzluebbers* [1999], and *Doran et al.* [1990].

Acknowledgement

This research was supported by the Director, Office of Science, Office of Biological and Environmental Research of the US Department of Energy under contract no. DE-AC02-05CH11231 as part of the Next Generation Ecosystem Experiment-Arctic project for JYT and WJR and the TES Soil Warming SFA for WJR and. GLM was supported by funding from the Department of Energy, Office of Biological and Environmental Research, Genomic Sciences

Program through the LLNL Microbes Persist Science Focus Area. ELB was supported by funding from the Department of Energy, Office of Biological and Environmental Research, Subsurface Biogeochemical Research Program through the LBNL Watershed Function Science Focus Area. Financial support does not constitute an endorsement by the Department of Energy of the views expressed in this study. The authors declare no conflicts of interest.

Author contributions

JYT conceived the idea and did the analysis; JYT, WJR, GLM and ELB discussed the analysis and wrote the paper.

References

Achat, D. L., L. Augusto, A. Gallet-Budynek, and D. Loustau (2016), Future challenges in coupled C-N-P cycle models for terrestrial ecosystems under global change: a review, *Biogeochemistry*, *131*(1-2), 173-202, doi:10.1007/s10533-016-0274-9.

Alberty, R. A. (1953), The relationship between Michaelis constants, maximum velocities and the equilibrium constant for an enzyme-catalyzed reaction, *J Am Chem Soc*, *75*(8), 1928-1932, doi:10.1021/ja01104a045.

Alberty, R. A., and G. G. Hammes (1958), Application of the theory of diffusion-controlled reactions to enzyme kinetics, *J Phys Chem-Us*, *62*(2), 154-159, doi:10.1021/j150560a005.

Almeida, J. S., M. A. M. Reis, and M. J. T. Carrondo (1995), Competition between nitrate and nitrite reduction in denitrification by pseudomonas-fluorescens, *Biotechnol Bioeng*, *46*(5), 476-484, doi:10.1002/bit.260460512.

Almeida, J. S., M. A. M. Reis, and M. J. T. Carrondo (1997), A unifying kinetic model of denitrification, *J Theor Biol*, *186*(2), 241-249, doi:10.1006/jtbi.1996.0352.

Arcus, V. L., E. J. Prentice, J. K. Hobbs, A. J. Mulholland, M. W. Van der Kamp, C. R. Pudney, E. J. Parker, and L. A. Schipper (2016), On the temperature dependence of enzyme-catalyzed rates, *Biochemistry-Us*, *55*(12), 1681-1688, doi:10.1021/acs.biochem.5b01094.

Atkins, P., L. Jones, and L. Laverman (2016), *Chemical Principles: The Quest for Insight*, Seventh ed., W.H. Freeman.

Briggs, G. E., and J. B. S. Haldane (1925), A note on the kinetics of enzyme action., *Biochem J*, *19*(2), 338-339, doi:10.1042/bj0190338.

Brutsaert, W. (2005), *Hydrology: An Introduction*, Cambridge University Press.

Cao, J. S. (2011), Michaelis-Menten equation and detailed balance in enzymatic networks, *J Phys Chem B*, *115*(18), 5493-5498, doi:10.1021/jp110924w.

Chen, J. W., et al. (2017), Impacts of chemical gradients on microbial community structure, *Isme J*, *11*(4), 920-931, doi:10.1038/ismej.2016.175.

Chou, K. C., and S. P. Jiang (1974), Studies on the rate of diffusion-controlled reactions of enzymes: spatial factor and force field factor, *Scientia Sinica*, *XVII*(5), doi:10.1360/ya1974-17-5-664.

Collatz, G. J., J. A. Berry, G. D. Farquhar, and J. Pierce (1990), The relationship between the rubisco reaction-mechanism and models of photosynthesis, *Plant Cell Environ*, *13*(3), 219-225, doi:10.1111/j.1365-3040.1990.tb01306.x.

Collatz, G. J., M. Ribas-Carbo, and J. A. Berry (1992), Coupled photosynthesis-stomatal conductance model for leaves of C4 plants, *Aust J Plant Physiol*, *19*(5), 519-538, doi:10.1071/Pp9920519.

Cramer, J. S. (2002), The origins of logistic regression*Rep.*, University of Amsterdam and Tinbergen Institute.

561 Dashko, S., N. Zhou, C. Compagno, and J. Piskur (2014), Why, when, and how did yeast evolve
562 alcoholic fermentation?, *Fems Yeast Res*, *14*(6), 826-832, doi:10.1111/1567-1364.12161.
563 de Alteriis, E., F. Carteni, P. Parascandola, J. Serpa, and S. Mazzoleni (2018), Revisiting the
564 Crabtree/Warburg effect in a dynamic perspective: a fitness advantage against sugar-induced cell
565 death, *Cell Cycle*, *17*(6), 688-701, doi:10.1080/15384101.2018.1442622.
566 Domingo-Felez, C., and B. F. Smets (2020), Modeling denitrification as an electric circuit
567 accurately captures electron competition between individual reductive steps: The activated
568 sludge model-electron competition model, *Environ Sci Technol*, *54*(12), 7330-7338,
569 doi:10.1021/acs.est.0c01095.
570 Doob, J. L. (1948), Renewal theory from the point of view of the theory of probability, *T Am*
571 *Math Soc*, *63*(May), 422-438, doi:10.2307/1990567.
572 Doran, J. W., L. N. Mielke, and J. F. Power (1990), Microbial activity as regulated by soil water-
573 filled pore space, in *International Society of Soil Science*, edited.
574 Droop, M. R. (1974), Nutrient status of algal cells in continuous culture, *J Mar Biol Assoc Uk*,
575 *54*(4), 825-855, doi:10.1017/S002531540005760x.
576 English, B. P., W. Min, A. M. van Oijen, K. T. Lee, G. B. Luo, H. Y. Sun, B. J. Cherayil, S. C.
577 Kou, and X. S. Xie (2006), Ever-fluctuating single enzyme molecules: Michaelis-Menten
578 equation revisited, *Nat Chem Biol*, *2*(2), 87-94, doi:10.1038/nchembio759.
579 Erickson, D. W., S. J. Schink, V. Patsalo, J. R. Williamson, U. Gerland, and T. Hwa (2017), A
580 global resource allocation strategy governs growth transition kinetics of Escherichia coli, *Nature*,
581 *551*(7678), 119-123, doi:10.1038/nature24299.
582 Etienne, T. A., M. Cocaign-Bousquet, and D. Ropers (2020), Competitive effects in bacterial
583 mRNA decay, *J Theor Biol*, *504*, doi:ARTN 110333 10.1016/j.jtbi.2020.110333.

584 Eyring, H. (1935), The activated complex and the absolute rate of chemical reactions, *Chem Rev*,
585 *17*(1), 65-77, doi:10.1021/cr60056a006.
586 Farquhar, G. D., S. V. Caemmerer, and J. A. Berry (1980), A biochemical-model of
587 photosynthetic CO2 assimilation in leaves of C3 species, *Planta*, *149*(1), 78-90,
588 doi:10.1007/Bf00386231.
589 Feynman, R. P., R. B. Leighton, and M. Sands (2011a), *The Feynman Lectures on Physics, Vol*
590 *II: Mainly Electromagnetism and Matter*, The New Millennium Edition ed., Basic Books; New
591 Millennium ed. Edition.
592 Feynman, R. P., R. B. Leighton, and M. Sands (2011b), *The Feynman Lectures on Physics, Vol*
593 *III: Quantum Mechanics*, The New Millennium Edition ed., Basic Books; New Millennium ed.
594 Edition.
595 Feynman, R. P., R. B. Leighton, and M. Sands (2011c), *The Feynman Lectures on Physics, Vol.*
596 *I: Mainly Mechanics, Radiation, and Heat*, The New Millennium Edition ed., Basic Books; New
597 Millennium ed. Edition.
598 Flamholz, A., E. Noor, A. Bar-Even, W. Liebermeister, and R. Milo (2013), Glycolytic strategy
599 as a tradeoff between energy yield and protein cost, *P Natl Acad Sci USA*, *110*(24), 10039-
600 10044, doi:10.1073/pnas.1215283110.
601 Franklin, O., E. K. Hall, C. Kaiser, T. J. Battin, and A. Richter (2011), Optimization of biomass
602 composition explains microbial growth-stoichiometry relationships, *Am Nat*, *177*(2), E29-E42,
603 doi:10.1086/657684.
604 Franzluebbers, A. J. (1999), Microbial activity in response to water-filled pore space of variably
605 eroded southern Piedmont soils, *Appl Soil Ecol*, *11*(1), 91-101, doi:Doi 10.1016/S0929-
606 1393(98)00128-0.

607 Garcia-Colin, L. S., L. F. del Castillo, and P. Goldstein (1989), Theoretical Basis for the Vogel-
608 Fulcher-Tammann Equation, *Phys Rev B*, *40*(10), 7040-7044, doi:10.1103/PhysRevB.40.7040.
609 Ghosh, K., and K. Dill (2010), Cellular proteomes have broad distributions of protein stability,
610 *Biophys J*, *99*(12), 3996-4002, doi:10.1016/j.bpj.2010.10.036.
611 Heinze, C., et al. (2019), ESD Reviews: Climate feedbacks in the Earth system and prospects for
612 their evaluation, *Earth Syst Dynam*, *10*(3), 379-452, doi:10.5194/esd-10-379-2019.
613 Holling, C. S. (1959), Some characteristics of simple types of predation and parasitism, *The*
614 *Canadian Entomologist*, *XCI*(7), 385-398.
615 Jin, Q., and C. M. Bethke (2007), The thermodynamics and kinetics of microbial metabolism,
616 *Am J Sci*, *307*(4), 643-677, doi:10.2475/04.2007.01.
617 Johnson, F. H., and I. Lewin (1946), The growth rate of E-Coli in relation to temperature,
618 quinine and coenzyme, *J Cell Compar Physl*, *28*(1), 47-75, doi:10.1002/jcp.1030280104.
619 Kirschbaum, M. U. F., and G. D. Farquhar (1984), Temperature-dependence of whole-leaf
620 photosynthesis in Eucalyptus-pauciflora Sieb ex Spreng, *Aust J Plant Physiol*, *11*(6), 519-538,
621 doi:10.1071/Pp9840519.
622 Kooijman, S. A. L. M. (1998), The Synthesizing Unit as model for the stoichiometric fusion and
623 branching of metabolic fluxes, *Biophys Chem*, *73*(1-2), 179-188, doi:10.1016/S0301-
624 4622(98)00162-8.
625 Koudriavstev, A. B., R. F. Jameson, and W. Linert (2001), *The law of mass action*, Springer,
626 Berlin Heidelberg, doi:10.1007/978-3-642-56770-4.
627 Labhsetwar, P., J. A. Cole, E. Roberts, N. D. Price, and Z. A. Luthey-Schulten (2014),
628 Heterogeneity in protein expression induces metabolic variability in a modeled Escherichia coli

population (vol 110, pg 14006, 2013), *P Natl Acad Sci USA*, *111*(2), 876-876, doi:10.1073/pnas.1323512111.

Labhsetwar, P., M. C. R. Melo, J. A. Cole, and Z. Luthey-Schulten (2017), Population FBA predicts metabolic phenotypes in yeast, *Plos Comput Biol*, *13*(9), doi:ARTN e1005728 10.1371/journal.pcbi.1005728.

Lawrence, D. M., et al. (2019), The Community Land Model Version 5: Description of new features, benchmarking, and impact of forcing uncertainty, *J Adv Model Earth Sy*, *11*(12), 4245-4287, doi:10.1029/2018ms001583.

Lu, Y., Q. H. Lai, C. Zhang, H. X. Zhao, K. Ma, X. B. Zhao, H. Z. Chen, D. H. Liu, and X. H. Xing (2009), Characteristics of hydrogen and methane production from cornstalks by an augmented two- or three-stage anaerobic fermentation process, *Bioresource Technol*, *100*(12), 2889-2895, doi:10.1016/j.biortech.2009.01.023.

Ma, S.-K. (1985), *Statistical Mechanics*, Wspc.

Madigan, M. T., J. M. Martinko, P. V. Dunlap, and D. P. Clark (2009), *Brock biology of microorganisms, twelfth edition*, Pearson Eduction, Inc. , 1301 Sansome Street, San Francisco, CA 94111.

Mansy, S. S., and J. W. Szostak (2008), Thermostability of model protocell membranes, *P Natl Acad Sci USA*, *105*(36), 13351-13355, doi:10.1073/pnas.0805086105.

Michaelis, L., and M. L. Menten (1913), The kinetics of the inversion effect, *Biochem. Z.*, *49*, 333-369.

Monod, J. (1949), The growth of bacterial cultures, *Annu Rev Microbiol*, *3*, 371-394, doi:10.1146/annurev.mi.03.100149.002103.

Murdoch, W. W. (1973), Functional response of predators, *J Appl Ecol*, *10*(1), 335-342.

652 Murphy, K. P., P. L. Privalov, and S. J. Gill (1990), Common features of protein unfolding and
653 dissolution of hydrophobic compounds, *Science*, *247*(4942), 559-561,
654 doi:10.1126/science.2300815.
655 Ninio, J. (1987), Alternative to the steady-state method - Derivation of reaction-rates from 1st-
656 passage times and pathway probabilities, *P Natl Acad Sci USA*, *84*(3), 663-667,
657 doi:10.1073/pnas.84.3.663.
658 O'Neill, R. V., D. L. Deangelis, J. J. Pastor, B. J. Jackson, and W. M. Post (1989), Multiple
659 nutrient limitations in ecological models, *Ecol Model*, *46*(3-4), 147-163, doi:10.1016/0304-
660 3800(89)90015-X.
661 Orth, J. D., I. Thiele, and B. O. Palsson (2010), What is flux balance analysis?, *Nat Biotechnol*,
662 *28*(3), 245-248, doi:10.1038/nbt.1614.
663 Qian, H. (2008), Cooperativity and specificity in enzyme kinetics: A single-molecule time-based
664 perspective, *Biophys J*, *95*(1), 10-17, doi:10.1529/biophysj.108.131771.
665 Ratkowsky, D. A., J. Olley, and T. Ross (2005), Unifying temperature effects on the growth rate
666 of bacteria and the stability of globular proteins, *J Theor Biol*, *233*(3), 351-362,
667 doi:10.1016/j.jtbi.2004.10.016.
668 Reuveni, S., M. Urbakh, and J. Klafter (2014), Role of substrate unbinding in Michaelis-Menten
669 enzymatic reactions, *P Natl Acad Sci USA*, *111*(12), 4391-4396, doi:10.1073/pnas.1318122111.
670 Riley, W. J., Z. M. Subin, D. M. Lawrence, S. C. Swenson, M. S. Torn, L. Meng, N. M.
671 Mahowald, and P. Hess (2011), Barriers to predicting changes in global terrestrial methane
672 fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated in CESM,
673 *Biogeosciences*, *8*(7), 1925-1953, doi:10.5194/bg-8-1925-2011.

674 Robertson, G. P., and P. M. Groffman (2015), Nitrogen transformations, in *Soil microbiology,*
675 *ecology and biochemistry*, edited by E. A. Paul, pp. 421-446, Academic Press, Burlington,
676 Massachusetts, USA.
677 Salamon, P., K. H. Hoffmann, S. Schubert, R. S. Berry, and B. Andresen (2001), What
678 conditions make minimum entropy production equivalent to maximum power production?, *J*
679 *Non-Equil Thermody*, *26*(1), 73-83, doi:Doi 10.1515/Jnetdy.2001.006.
680 Salamon, P., T. N. F. Roach, and F. L. Rohwer (2017), The ladder theorem, paper presented at
681 14th Joint European Thermodynamics Conference, Budapest, May 21-25.
682 Sawle, L., and K. Ghosh (2011), How do thermophilic proteins and proteomes withstand high
683 temperature?, *Biophys J*, *101*(1), 217-227, doi:10.1016/j.bpj.2011.05.059.
684 Schipper, L. A., J. K. Hobbs, S. Rutledge, and V. L. Arcus (2014), Thermodynamic theory
685 explains the temperature optima of soil microbial processes and high Q(10) values at low
686 temperatures, *Global Change Biol*, *20*(11), 3578-3586, doi:10.1111/gcb.12596.
687 Schmidt-Rohr, K. (2018), How batteries store and release energy: explaining basic
688 electrochemistry, *J Chem Educ*, *95*(10), 1801-1810, doi:10.1021/acs.jchemed.8b00479.
689 Shaver, G. R., and J. M. Melillo (1984), Nutrient budgets of marsh plants - efficiency concepts
690 and relation to availability, *Ecology*, *65*(5), 1491-1510, doi:10.2307/1939129.
691 Shuttleworth, W. J., and J. S. Wallace (1985), Evaporation from sparse crops - an energy
692 combination theory, *Q J Roy Meteor Soc*, *111*(469), 839-855, doi:10.1256/smsqj.46909.
693 Smith, O. L. (1976), Nitrogen, phosphorus, and potassium utilization in plant-soil system -
694 analytical model, *Soil Sci Soc Am J*, *40*(5), 704-714,
695 doi:10.2136/sssaj1976.03615995004000050029x.

696 Smith, O. L. (1979), Application of a model of the decomposition of soil organic-matter, *Soil*
697 *Biol Biochem*, *11*(6), 607-618, doi:10.1016/0038-0717(79)90028-2.
698 Stumm, W., and J. J. Morgan (1996), *Aquatic chemistry: chemical equilibria and rates in natural*
699 *waters*, Wiley.
700 Swenson, H., and N. P. Stadie (2019), Langmuir's theory of adsorption: a centennial review,
701 *Langmuir*, *35*(16), 5409-5426, doi:10.1021/acs.langmuir.9b00154.
702 Taiz, L., and E. Zeiger (2006), *Plan physiology, 4th edn*, Sinauer Associates, Inc., Sunderland,
703 MA 01375 USA.
704 Tang, J. Y. (2015), On the relationships between the Michaelis-Menten kinetics, reverse
705 Michaelis-Menten kinetics, equilibrium chemistry approximation kinetics, and quadratic
706 kinetics, *Geosci Model Dev*, *8*(12), 3823-3835, doi:10.5194/gmd-8-3823-2015.
707 Tang, J. Y., and W. J. Riley (2013), A total quasi-steady-state formulation of substrate uptake
708 kinetics in complex networks and an example application to microbial litter decomposition,
709 *Biogeosciences*, *10*(12), 8329-8351, doi:10.5194/bg-10-8329-2013.
710 Tang, J. Y., and W. J. Riley (2017), SUPECA kinetics for scaling redox reactions in networks of
711 mixed substrates and consumers and an example application to aerobic soil respiration, *Geosci*
712 *Model Dev*, *10*(9), 3277-3295, doi:10.5194/gmd-10-3277-2017.
713 Tang, J. Y., and W. J. Riley (2019a), Competitor and substrate sizes and diffusion together
714 define enzymatic depolymerization and microbial substrate uptake rates, *Soil Biol Biochem*, *139*,
715 doi:ARTN 107624 10.1016/j.soilbio.2019.107624.
716 Tang, J. Y., and W. J. Riley (2019b), A theory of effective microbial substrate affinity
717 parameters in variably saturated soils and an example application to aerobic soil heterotrophic
718 respiration, *J Geophys Res-Biogeo*, *124*(4), 918-940, doi:10.1029/2018jg004779.

719 Thomsen, J. K., T. Geest, and R. P. Cox (1994), Mass-spectrometric studies of the effect of pH
720 on the accumulation of intermediates in denitrification by paracoccus-denitrificans, *Appl Environ*
721 *Microb*, *60*(2), 536-541, doi:10.1128/Aem.60.2.536-541.1994.
722 Tilman, D. (1982), *Resource competition and community structure*, 1st ed., 296 pp., Princeton
723 University Press.
724 Unden, G., and J. Bongaerts (1997), Alternative respiratory pathways of Escherichia coli:
725 Energetics and transcriptional regulation in response to electron acceptors, *Bba-Bioenergetics*,
726 *1320*(3), 217-234, doi:10.1016/S0005-2728(97)00034-0.
727 Vallis, G. K. (2006), *Atmospheric and Oceanic Fluid Dynamics: Fundamentals and Large-scale*
728 *Circulation*, 1 ed., Cambridge University Press.
729 von Smoluchowski, M. (1917), Versuch einer mathematischen theorie der koagulationkinetik
730 kolloider loesungen., *Z Phys Chem*, *92*, 129–132.
731 Wu, Y. H., J. Walker, D. Schwede, C. Peters-Lidard, R. Dennis, and W. Robarge (2009), A new
732 model of bi-directional ammonia exchange between the atmosphere and biosphere: Ammonia
733 stomatal compensation point, *Agr Forest Meteorol*, *149*(2), 263-280,
734 doi:10.1016/j.agrformet.2008.08.012.
735