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**PERSPECTIVE**

# How Michaelis–Menten kinetics can represent ecosystem-scale respiration: scale and applicability

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## 1. Introduction

Terrestrial ecosystem respiration ($R_e$) is a crucial component of the carbon cycle and is expected to increase with anthropogenic warming [1]. The temperature response of $R_e$ is typically parameterized using temperature sensitivity $Q_{10}$, which describes the increase in respiration with a 10 K rise in temperature. This is commonly expressed as [2]

$$Q_{10} = \frac{R_e\left(T+10\right)}{R_e\left(T\right)} = \mathrm{e}^{\frac{E_a}{k}\frac{10}{T(T+10)}}. \tag{1}$$

However, the Arrhenius equation [3] provides a more mechanistic foundation by explicitly incorporating activation energy ($E_a$), which governs the temperature dependence of biochemical reactions,

$$R_e = a e^{\frac{-E_a}{kT}}, \tag{2}$$

where $R_e$ is ecosystem respiration, $a$ is a reference respiration rate, $E_a$ is activation energy (eV), $k$ is Boltzmann's constant ($8.62 \times 10^{-5}$ eV $\mathrm{K}^{-1}$), and $T$ is temperature ($K$) (table 1).

The respiration increase largely determines the future direction of the terrestrial-atmosphere carbon balance [4, 5]. However, our current understanding of the mechanisms driving $Q_{10}$ variation across latitudes and biomes is still insufficient [6, 7]. As a result, it remains difficult to constrain predictions of future $R_e$ dynamics [4, 8].

The Michaelis–Menten (MM) kinetics [9], developed to describe enzyme-catalyzed reactions, is a cornerstone to understand biochemical processes at cellular and molecular levels. This model effectively captures the relationship between substrate concentration and reaction rates, simplifying complex biochemical interactions into manageable mathematical expressions using the key parameters $V_{\max}$ (maximum reaction rate) and $K_m$ (substrate concentration at half the maximum rate). The general form of the MM equation is

$$R_e = \frac{V_{\max} \cdot S}{K_m + S} \qquad (3)$$

where $S$ represents the substrate concentration. The applicability of such a microscopic model to large-scale ecosystem processes can be questioned [10]. However, most Earth system models already incorporate the Farquhar–von Caemmerer–Berry (FvCB) biochemical model [11], which is grounded in MM kinetics, to simulate photosynthesis at ecosystem or larger scales. By contrast, the description of respiration processes over large ecosystem scale still predominantly relies on more empirical models [1, 12, 13], projecting an exponential temperature response with Arrhenius [13] or $Q_{10}$ types of functions [3].

The FvCB model is fundamentally a leaf-scale approach, which various Land Surface Models (LSMs) have extended to the canopy level through various scaling methods [14, 15]. Early models treated the canopy as a simple 'big leaf', but more advanced models incorporate sunlit and shaded leaves or even use numerical multi-layer approaches to capture vertical gradients in photosynthetic capacity, such as the exponential decrease of $V_{\max}$ with canopy depth [15]. Ecosystem-level respiration modeling is more complex, involving diverse components like stems, roots, microbes, and animals, with both anaerobic and aerobic pathways [6]. Thus, while upscaling photosynthesis has been refined, questions remain about the applicability of MM kinetics for capturing ecosystem-level respiration dynamics.

Despite the example of photosynthesis, the complexity of ecosystem respiration—which encompasses autotrophic processes in plants and heterotrophic activities of soil microbes—poses challenges for applying a simplified model like MM kinetics at large scales [10]. To enhance its effectiveness, we propose temperature and substrate availability (e.g. soil organic carbon) as key predictors of respiration rates. Temperature regulates enzymatic reaction rates in both autotrophic and heterotrophic pathways, while substrate availability provides the fuel for microbial respiration. Additionally, soil moisture should be considered, as it influences substrate accessibility and microbial activity in many ecosystems.

Ecosystem respiration operates across a wide range of temporal and spatial scales, interacting with dynamics and spatially heterogeneous environmental factors like temperature, moisture, and substrate availability [6, 16], which further complicate the application of MM kinetics at ecosystem scale [16, 17]. One particularly challenging issue is the nonlinear response of ecosystem respiration to moisture, where the precipitation thresholds can drastically shift ecosystems between water-limited and energy-limited states [18, 19]. This raises the question: Can MM kinetics adequately capture the nonlinear dynamics of ecosystem respiration at large scales, especially in the context of a precipitation threshold? This paper aims to discuss arguments against and in favor of this question, drawing on existing research and data to explore the strengths and limitations of using this model to predict ecosystem-level carbon cycling.

## 2. Problems of using MM kinetics for large-scale ecosystem respiration

A primary challenge in applying MM kinetics to ecosystem respiration lies in scalability. Originally developed for enzyme-level reactions, MM kinetics does not naturally extend to larger, complex systems like ecosystems. Ecosystems involve numerous organisms and processes, each with unique contributions to respiration and individual $V_{\max}$ and $K_m$ parameters. Simple summing or averaging of these interactions across an entire ecosystem does not typically preserve the original MM form, as parameters like $V_{\max}$ and $K_m$, which are well-defined in controlled conditions, are difficult to apply in dynamic and heterogeneous environments [8, 20, 21]. Choosing an appropriate ecosystem substrate, then accounting for the variability in substrate concentrations and enzyme activities across spatial and temporal scales, complicates the definition of ecosystem-wide MM parameters.

Despite these challenges, recent research indicates it may be possible to derive 'effective' large-scale rates that retain the MM form by accounting for ecosystem heterogeneity and dynamic variability. By averaging localized MM parameters (e.g. $V_{\max}$ and $K_m$) while accounting for spatial and temporal variations, MM kinetics can be approximated at broader scales. This approach, which explicitly addresses ecosystem-level complexities, suggests that MM kinetics may remain valid at large scales, though not necessarily with parameters directly interpretable in the same way as in controlled lab settings [22, 23]. However, more research is needed to establish the conditions, under which these effective rates reliably capture ecosystem-scale dynamics.

Ecosystem respiration involves a diverse array of organisms—plants, microbes, animals—each operating under varying physiological and environmental constraints [4, 24]. MM kinetics assumes stable conditions for enzyme-substrate interactions, whereas ecosystems are characterized by fluctuations in substrate availability, temperature, and moisture. Additionally, respiration of autotrophs and heterotrophs contribute differently to total $CO_2$ fluxes [25, 26], further complicating the application of a uniform model.

Another issue is the timescale. MM kinetics describes rapid enzyme reactions occurring over milliseconds, while ecosystem respiration operates on much longer timescales influenced by nutrient cycling, biomass turnover, and other slower processes

**Table 1.** Comparison of Michaelis–Menten and Arrhenius Models in the Context of Ecosystem Respiration $R_e$.

| Model | Michaelis–Menten (MM) model | Arrhenius model |
|---|---|---|
| Key parameters | -$V_{\max}$ (maximum enzyme activity) is typically represented by ecosystem respiration potential under optimal conditions.<br>- $K_M$ (substrate affinity) is often linked to environmental factors like soil moisture or carbon availability. | - Activation energy ($E_a$) is often replaced with an empirical temperature sensitivity parameter.<br>- The pre-exponential factor can be influenced by substrate availability and microbial biomass. |
| Background | - Describes the rates of enzyme reactions depending on substrate concentration<br>- Substrate concentration is the main factor of the reaction rate<br>- Is based on 2 parameters: reflecting affinity of enzyme to the substrate ($K_M$) and maximal reaction rate at substrate saturation ($V_{\max}$).<br>- Is independent of time | - Describes the rates of chemical reactions depending on temperature<br>- Temperature changes are the main factor of the reaction rate<br>- Assumed to be independent of the reaction type and agents. |
| Advantages | - Captures enzyme-substrate interactions, suitable for biological systems.<br>- Considers substrate saturation, including soil moisture via substrate concentration.<br>- Allows temperature effects via $V_{\max}$ and $K_M$ adjustments. | - Directly models temperature effects; ideal when temperature is the primary driver.- Simple, broadly applicable, with straightforward calculations. |
| Limitations | - Temperature effects are indirect, requiring separate functions for $V_{\max}$ and $K_M$.<br>- Challenging to scale due to non-linearity and substrate variability. | - Ignores substrate saturation, limiting accuracy in systems with varying resources.<br>- May oversimplify reactions influenced by enzyme kinetics and resource availability.<br>- Less accurate where substrate controls the reaction rates.<br>- Ignores denaturation of enzymes by warming |

[27]. Using MM kinetics at this scale can reduce it to an empirical tool, alienated from its enzyme-level theoretical foundation.

In this context, the Arrhenius equation provides an alternative approach that scales more naturally to ecosystem-level respiration. Widely used in ecosystem studies, the Arrhenius model does not rely on detailed enzyme mechanisms [28, 29] but instead captures temperature effects on respiration at a broader scale. Though less mechanistic than MM kinetics, it offers a practical framework for modeling of ecosystem dynamics (table 1).

In summary, ecosystem respiration involves complex biological processes across multiple scales. MM kinetics, while effective at the enzyme level, relies on assumptions that rarely hold in ecosystems. Scaling MM kinetics to the ecosystem level oversimplifies real-world variability, leading to inaccuracies. Nonlinear models like MM kinetics do not scale predictably, and the emergent behaviors of ecosystems cannot be fully captured by models designed for individual enzyme reactions. As such, while MM kinetics offers an intriguing conceptual framework, it often results in a loss of accuracy and theoretical coherence when applied to larger scales (table 1).

## 3. Possibilities to use MM kinetics for large-scale ecosystem respiration

The MM kinetics framework, traditionally applied to enzyme-catalyzed reactions at the microbial or molecular level, has increasingly been adapted for use in ecosystem-scale studies, particularly in understanding carbon cycling and ecosystem respiration. Several studies provide strong evidence that MM kinetics can effectively describe processes involved in soil organic matter (SOM) decomposition, extracellular enzyme activities, and temperature sensitivities in ecosystems.

(i) *Temperature Sensitivity and Soil Enzyme Kinetics* In German *et al* [30], the MM kinetic framework was applied to study the activity of extracellular hydrolytic enzymes across a latitudinal gradient from boreal forests to tropical rainforests. These enzymes are crucial for SOM decomposition. Although the study was conducted under controlled conditions, it demonstrated that $V_{\max}$ and $K_M$ of enzymes involved in SOM degradation, such as $\beta$-glucosidase and cellobiohydrolase, were both temperature-sensitive, with

$Q_{10}$ values indicating strong increases in $V_{\max}$ across temperatures.

While $K_M$ had lower temperature sensitivity, its variability showed that MM kinetics can effectively capture enzyme responses to temperature changes, offering preliminary insights relevant to soil C dynamics. This study suggests that MM kinetics, when properly adapted, offers a mechanistic framework to understand soil carbon loss under global warming. However, further research is needed to validate MM's applicability at ecosystem scales, where environmental complexity and natural soil variability play a larger role.

(ii) *Nonlinear Temperature Sensitivity and the Canceling Effect*

The concept of a 'canceling effect', first introduced by Davidson and Janssens [6], describes how differing temperature sensitivities between $V_{\max}$ and $K_M$ can dampen the overall temperature response of enzymatic reactions under limited substrate conditions. Razavi *et al* [31] expanded on this concept by examining the nonlinear temperature sensitivity of soil enzymes involved in SOM decomposition in loamy haplic Luvisol. Their study observed that while $V_{\max}$ for enzymes like $\beta$-glucosidase and cellobiohydrolase increased nonlinearly between 10 and 15 °C, a reduction in enzyme-substrate affinity (increased $K_M$) at temperatures above 25 °C led to a sharp decline in overall enzyme activity. This canceling effect was particularly evident at low substrate concentrations and moderate temperatures, suggesting a natural regulatory mechanism that could buffer the effects of global warming on SOM decomposition rates.

Razavi *et al* [31] studied the nonlinear behavior of soil enzyme kinetics in response to warming. The MM kinetics framework allowes to demonstrate how temperature thresholds affect enzyme functions, which in turn affects soil respiration. Importantly, the canceling effect can offset some of the warming-induced acceleration in SOM decomposition, especially in temperate regions, indicating that MM kinetics can incorporate nuanced responses to temperature changes in predictive models. This study underscores the necessity of including such nonlinear dynamics in Earth system models to improve predictions at regional and global scales.

Blagodatskaya *et al* [32] expanded on the canceling effect by examining the temperature sensitivity of SOM decomposition along an altitudinal gradient on Mount Kilimanjaro. They observed that, as altitude increased, so did $K_M$, which counteracted the increase in $V_{\max}$ with temperature. This phenomenon resulted in a 'canceling effect', reducing decomposition rates at higher altitudes and indicating a thermal adaptation in cold climates. By defining threshold substrate concentrations ($S_{\mathrm{crit}}$), below which decomposition becomes temperature-insensitive, the soils in cold climates may be less sensitive to global warming than those in warmer climates. These findings underscore how environmental gradients influence the applicability of MM kinetics for predicting large-scale SOM decomposition in response to climate change.

(iii) *Nitrogen Fertilization and Forest Ecosystems*

A similar approach was taken by Stone *et al* [33], who used MM kinetics to explore the effects of nitrogen fertilization on soil enzymes in temperate forests. The long-term nitrogen addition strongly increased the $V_{\max}$ values of multiple enzymes, including $\alpha$-glucosidase and $\beta$-glucosidase, in forest soils. Interestingly, nitrogen fertilization also affected $K_M$ values, showing that MM kinetics could capture both potential reaction rate and substrate affinity changes in response to nutrient inputs.

In addition, $V_{\max}$ and $K_M$ were sensitive to temperature changes, with $Q_{10}$ values ranging from 1.6 to 2.3 for $V_{\max}$, suggesting a robust increase in substrate degradation rates at higher temperatures. The application of MM kinetics in this context provided insights into how nitrogen deposition could exacerbate carbon release from forest soils under warming conditions. This underscores the utility of MM kinetics for predicting ecosystem respiration responses to both nutrient enrichment and climate change.

(iv) *Ecosystem-Level Modeling and Prediction*

These studies not only demonstrate the relevance of MM kinetics to understand enzyme behavior in ecosystems but also show that MM-based models can scale up from microbial processes to predict ecosystem-wide responses. In both microbial and ecosystem-scale applications, temperature sensitivity and nutrient effects were captured through MM parameters, enabling predictions of $CO_2$ release and soil respiration under varying environmental conditions.

For example, German *et al* [30] tested the hypothesis that enzymes from higher latitudes (cooler climates) would be more sensitive to temperature than those from lower latitudes (warmer climates). They found that enzymes in cooler climates have greater temperature sensitivities, validating the potential of MM kinetics to capture regional variations in enzyme activity and carbon cycling. This study demonstrates that local adaptations of microorganisms to produce enzymes efficient under specific conditions can influence ecosystem responses to climate change, further supporting the application of MM models at larger scales.

These successful examples demonstrate the viability of MM kinetics in capturing ecosystem respiration thresholds and carbon cycling dynamics. By adapting parameters such as $V_{\max}$ and $K_M$ to account for temperature and nutrient conditions, researchers have shown that MM kinetics can effectively model ecosystem-scale processes. This challenges the notion that MM kinetics are confined to small-scale biological systems and suggests that, with proper parameterization, MM-based models can predict critical carbon cycle feedbacks in a changing climate.

## 4. New data supporting the use of MM kinetics

Our recent study [18]investigated the mechanisms behind the apparent $Q_{10}$ decline for drier ecosystems, represented by larger Budyko dryness index (DI), and further supported the application of MM kinetics at large ecosystem scale. The DI, defined as the ratio of potential evapotranspiration to precipitation [34], was shown to demarcate temperature and precipitation dependence of ecosystem respiration. When DI $< 1$, $R_e$ is temperature-sensitive, whereas when DI $> 1$, $R_e$ becomes precipitation-limited and its sensitivity to temperature is reduced.

Most current LSMs assume the temperature and moisture effects on $R_e$ to be independent [1]. However, recent observations challenge this, showing that the temperature sensitivity $Q_{10}$ varies with moisture conditions [18, 19] Using FLUXNET2015 data [35] from 212 global sites, we identified DI $= 1$ as the threshold at which $R_e$ shifts from temperature-driven (wet conditions) to moisture-driven (dry conditions). Specifically, in wetter environments (DI $< 1$), $Q_{10}$ decreases linearly with increasing DI, while in drier environments (DI $> 1$), $Q_{10}$ remains low and stable [18].

At the ecosystem scale, the temperature sensitivity of $R_e$ can be interpreted through the lens of MM kinetics, which effectively models the interactions between substrate availability (e.g. carbon) and enzyme-mediated processes over that scale. The Arrhenius equation (table 1), traditionally used to describe temperature sensitivity, was also applied to calculate activation energy ($E_a$) across sites with varying DI values. In wet conditions (DI $<1$), $E_a$ decreases linearly with increasing DI, whereas in dry conditions (DI $> 1$), $E_a$ remains low and nearly constant (figure 1). This suggests that the probability of reaction occurrence by overcoming the energy barrier (activation energy) increases more rapidly in wet conditions than in dry ones, leading to greater temperature sensitivity of $R_e$ in moist environments.

To explain why $Q_{10}$, or $E_a$ in the Arrhenius model, depend on DI, the MM kinetics model (table 1) provides a compelling framework. In wet conditions (DI $< 1$), where substrate (e.g. carbon) is abundant, the system approaches $V_{\max}$, and the temperature sensitivity of $R_e$ is driven primarily by $V_{\max}(T)$. In dry conditions (DI $> 1$), substrate availability diminishes, and $R_e$ becomes decoupled from temperature as the MM kinetics equation suggests—low substrate concentration leads to $T$-insensitivity (figure 1). This occurs because the temperature sensitivity of $V_{\max}(T)$ is counteracted by the temperature response of $K_M(T)$, leading to the ‘canceling effect’ also found in laboratory studies[31].

We also examined the site-specific maximum ($\mathrm{LAI}_{\max}$) as a proxy for ecosystem productivity and substrate availability. In wet sites (DI $< 1$), $\mathrm{LAI}_{\max}$ remains consistently high, but it decreases sharply near DI $= 1$ and continues to decline as DI increases, reflecting reduced biomass and microbial activity under water-limited conditions (figure 1). These findings are consistent with decreased carbon flux between soil, canopy, and atmosphere under dry conditions [36, 37], further decoupling $R_e$ from temperature under such water limitation, and supporting the utility of MM kinetics in modeling these processes at ecosystem scale.

In summary, analysis of FLUXNET data underscores the potential of MM kinetics to explain the shifting temperature sensitivity of ecosystem respiration across moisture gradients, providing mechanistic insights into how substrate availability and enzyme kinetics interact under varying climatic conditions.

## 5. Future directions: extending MM kinetics to ecosystem respiration

While MM kinetics has long been applied to estimate gross primary production (GPP, photosynthesis) across various time and spatial scales, its application to ecosystem respiration remains limited. The MM application difference between assessments of GPP and ecosystem respiration underscores an important gap in current ecological modeling, one that presents both challenges and opportunities for future research. Expanding MM kinetics to more comprehensively model ecosystem respiration could strongly advance our understanding of the carbon cycle, especially in the context of climate change.

### 5.1. Application of MM kinetics to GPP vs. ecosystem respiration

The broad application of MM kinetics to GPP has yielded valuable insights into photosynthetic processes and carbon uptake. However, ecosystem respiration—which includes respiration of both autotrophs (plants) and heterotrophs (mostly microorganisms)—has not been similarly modeled with MM kinetics.

*Understanding the difference*: One reason for this difference may lie in the relative simplicity of photosynthetic processes compared to the complex and variable factors that influence respiration. GPP is driven by relatively predictable factors like light, temperature, and $CO_2$ concentration. Ecosystem respiration, however, is influenced by a wider array of environmental and biological variables, such as temperature, moisture, substrate availability, microbial activity [38, 39], and plant physiology. This complexity makes it more difficult to apply a straightforward MM framework to respiration.

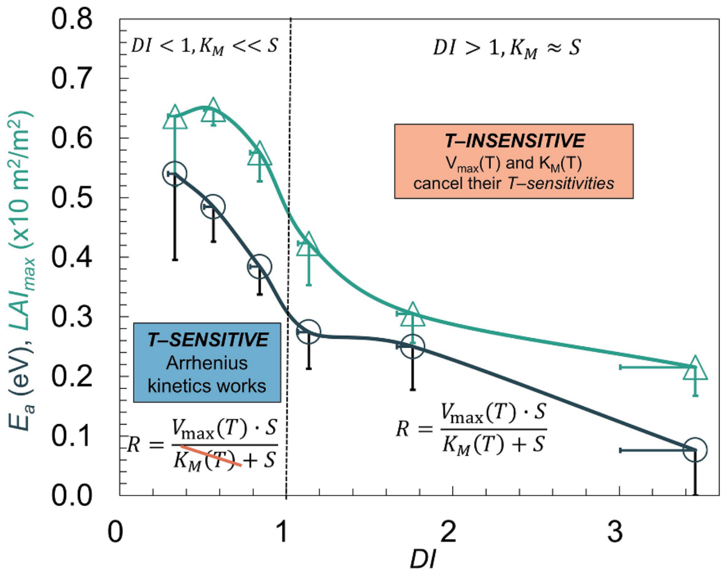

**Figure 1.** Mechanistic explanation of a temperature-sensitivity moisture threshold using Michaelis–Menten (MM) kinetics. 212 sites of FLUXNET2015 were grouped by dryness index (DI) into six intervals: $0 < \text{DI} < 0.4$ (9 sites); $0.4 < \text{DI} < 0.7$ (61 sites); $0.7 < \text{DI} < 1.0$ (58 sites); $1.0 < \text{DI} < 1.4$ (38 sites); $1.4 < \text{DI} < 2.2$ (23 sites); and $\text{DI} > 2.2$ (23 sites). The activation energy $E_a$ and its variability are high under moist climates when $DI < 1$, where substrate availability ($S$) is much lower than the half-saturation constant ($K_M$), making the MM model highly sensitive to temperature. Under dry climates with $\text{DI} > 1$, $K_M \approx S$, and the temperature sensitivities of $V_{\max}$ and $K_M$ largely cancel out, leading to a lower and more stable $E_a$. Maximum monthly leaf area index (LAI) was used as a proxy for substrate availability ($S$). The whiskers on each data point represent standard errors. The equations in the figure illustrate MM kinetics depending on moisture conditions, explaining why $E_a$ varies across DI. For each DI group, we estimate $E_a$ using $E_a = \frac{1}{kT}\ln\left(\frac{a}{R_e}\right)$ based on temperature and $R_e$ data.

*Potential for Extension*: Despite these challenges, the potential to extend MM kinetics to model ecosystem respiration is considerable. Doing so would provide a more mechanistic and process-based representation of both major components of the carbon cycle, enabling more accurate predictions of net ecosystem exchange depending on environmental conditions.

### 5.2. Challenges in applying MM kinetics to ecosystem respiration

Several challenges must be overcome to apply MM kinetics to ecosystem respiration effectively.

*Heterogeneity of Respiratory Processes*: Respiration involves both autotrophic (plant) and heterotrophic (microbial) components, each of which responds specifically to environmental factors. The MM parameters ($V_{\max}$ and $K_M$) would need to be calibrated separately for these processes, which poses a methodological challenge.

*Approaches for Calibration*: In controlled laboratory or greenhouse experiments, autotrophic and heterotrophic respiration can be isolated using root exclusion methods, stable isotope labeling, or chamber-based incubations. These techniques allow estimation of species- or functional-group-specific MM parameters under well-defined conditions. However, scaling these parameters to the ecosystem level is more complex due to spatial heterogeneity and environmental variability.

*Scaling Complexity*: Bridging this gap requires integrating multiple data sources, including ecosystem-scale flux measurements (e.g. eddy covariance), soil chamber experiments, and isotope tracing, to differentiate autotrophic and heterotrophic contributions [40]. Machine learning techniques can further aid in inferring effective MM parameters across diverse environmental conditions. Additionally, process-based modeling approaches can incorporate findings from controlled laboratory incubations and greenhouse experiments to improve parameterization at ecosystem scales. Future research should focus on developing scalable techniques that account for spatial and temporal variability in respiration dynamics, ensuring that MM kinetics can be effectively applied across ecosystems.

*Temperature Sensitivity*: Ecosystem respiration, especially heterotrophic respiration, is highly sensitive to temperature changes. MM kinetics, which already incorporates temperature effects on enzyme activity, could be a valuable framework for modeling temperature-respiration relationships, especially under changing climate conditions. However, capturing this sensitivity accurately at large scales will require advanced coupling of MM models with climate and hydrological variables.

### 5.3. Toward a unified framework for carbon cycle modeling

One promising direction for future research is the development of a unified framework that applies MM kinetics to both GPP and ecosystem respiration. This would allow for more integrated and mechanistic modeling of carbon fluxes at ecosystem and global scales as well as application of partly the same parameters for GPP and $R_e$.

*Parameterization for Respiration*: Developing robust parameterizations of MM kinetics for ecosystem respiration is a key research priority. This includes determining appropriate effective ecosystem-scale $V_{\max}$ and $K_M$ values for respiration across biomes and environmental conditions. Rather than parameterizing arbitrary 'segments' of the biome, a more effective approach would be to infer emergent MM parameters at the ecosystem scale using integrative techniques. Ecosystem-scale flux measurements (e.g. eddy covariance), soil chamber data, and machine learning methods can be leveraged to constrain effective MM kinetics. Additionally, process-based modeling approaches can integrate controlled experimental findings with field observations, improving parameterization across environmental gradients while minimizing equifinality issues [38, 39].

*Dynamic Feedbacks*: Rather than treating autotrophic and heterotrophic respiration as fully independent processes, an alternative approach is to model their interactions explicitly within an MM-based framework. Heterotrophic respiration depends dynamically on carbon inputs by autotrophs, particularly in the rhizosphere, where root exudates fuel microbial activity [41–43]. While the Krebs cycle is a shared metabolic pathway for respiration, differences in substrate availability, environmental responses, and spatial distribution justify distinguishing between autotrophic and heterotrophic contributions. However, to balance complexity and tractability, an effective approach could involve coupling MM-based GPP and respiration parameterizations while integrating empirical constraints. Rather than explicitly separating autotrophic and heterotrophic respiration in a highly complex framework, models could leverage emergent dependencies of total ecosystem respiration on GPP, ensuring that carbon exchange between plants and microbes is adequately represented while maintaining dynamic feedback.

### 5.4. Leveraging data for improved model calibration

Advances in satellite-based remote sensing and networks like FLUXNET offer new opportunities to refine MM kinetics at the ecosystem scale. High-resolution datasets, such as eddy covariance measurements, provide critical substrate, temperature, and moisture data to calibrate MM models at regional and global levels.

Machine learning algorithms can further aid this effort by automating parameter estimation for $V_{\max}$ and $K_M$ and detecting patterns that traditional models may overlook. By integrating AI tools with large-scale data, we might be able to better predict how ecosystems respond to environmental changes and identify critical thresholds, refining MM-based approaches to ecosystem respiration modeling.

### 5.5. Predicting ecosystem resilience and carbon balance

Ultimately, applying MM kinetics to ecosystem respiration could help to predict ecosystem resilience and the response of carbon cycling to climate change [1, 5, 7, 18].

*Thresholds and Tipping Points*: As ecosystems experience increasing stress due to climate change, MM kinetics could help identify critical thresholds or tipping points where respiration accelerates, leading to a net release of carbon. This could be particularly important for understanding carbon feedbacks in vulnerable ecosystems like boreal forests and peatlands.

*Improving Global Carbon Budgets*: Extending MM kinetics to ecosystem respiration could enable more accurate estimates of global carbon budgets by providing a mechanistic basis for predicting both carbon uptake and release. This would improve projections of how ecosystems respond to climate scenarios and help guide climate mitigation strategies.

In summary, resolving the issues underlying the current difference in application of MM kinetics between GPP and ecosystem respiration is an important research direction. By extending MM kinetics to ecosystem respiration, researchers can develop a more mechanistic understanding of the carbon cycle at larger scales, ultimately improving predictions of ecosystem responses to climate change. Overcoming the challenges associated with heterogeneity, scaling, and data availability will be essential, but the potential benefits for carbon cycle modeling and climate projections are significant.

## Data availability statement

The FLUXNET2015 Dataset used here are publicly available at https://fluxnet.org/data/fluxnet2015-dataset/. The MCD15A3H data are publicly available at https://e4ftl01.cr.usgs.gov/MOTA/. All other data that support the plots within this paper and other findings of this study are available from the corresponding author upon reasonable request.

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