Sensitivity of Soil Organic Carbon to the Change in Climate on the Tibetan Plateau

Von der Naturwissenschaftlichen Fakultät der
Gottfried Wilhelm Leibniz Universität Hannover

zur Erlangung des Grades
Doktorin der Naturwissenschaften (Dr. rer. nat.)

genehmigte Dissertation
von

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2022

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Tag der Promotion:	25.03.2022

Summary

Soil organic carbon, as the main terrestrial component in the Earth's carbon cycle, has a profound effect on the accumulation of CO_2 in atmosphere and consequently on global warming. In the alpine grasslands of the Tibetan Plateau, the decomposition rate of soil organic carbon is controlled by several biotic and abiotic factors, which mostly change simultaneously and often leads to freezing and thawing cycles. However, it is highly uncertain whether the temperature sensitivity of decomposition around the freezing point of water is similar as in higher temperature ranges.

The main objective of this dissertation is to evaluate the effects of simultaneous changes in three climate factors on soil organic carbon decomposition rates using an incubation experiment and a biogeochemical model. Due to the large divergence between empirical and model-based approaches in predicting the effects of abiotic factors on soil carbon dynamics, this dissertation first provides an approach to uncover some sources of uncertainty in estimated SOC processes in alpine grasslands.

In this study, I evaluated the complexity of the model required to represent the dynamics of carbon observed in incubation studies. Information theory metrics including AIC and BIC, as well as carbon particle mean transit time, were used as criteria to select models that better predict the data without making additional assumptions about model structure.

These analyses showed that during the limited course of an incubation experiment, the amount of transfer between the different SOC pools is negligible and adding these parameters to the model could lead to over-parameterization. These findings suggest that carbon models with less parameterized structures, such as the one-pool model or the two-pool model with parallel structure, that does not account for transfers between pools, indeed have better predictive power in describing the decomposition of carbon fractions while following the principle of parsimony.

The aforementioned information was later used to evaluate the sensitivity of SOC degradation rates to changes in soil temperature, soil moisture, and oxygen availability, especially at low temperatures. Functions from the Dual Arrhenius-Michaelis-Menten model (DAMM) were implemented in a one-pool model of SOC represented as first-order differential equation with time-dependent coefficients. A manipulative freeze-thaw cycle was imposed on a soil from Tibetan grasslands, in addition to soil moisture treatments that ranged from extremely dry to fully saturated, under both oxic and anoxic conditions.

The intrinsic sensitivities indicated that temperature (energy) is the main factor limiting decomposition in cold environments, provided moisture and oxygen are sufficiently available. However, the intrinsic sensitivities related to soil moisture and oxygen concentration are only relevant in very narrow ranges when soils are nearly dry or partially anoxic, and small changes within these narrow ranges can result in large changes in decomposition rates.

Zusammenfaßung

Organischer Kohlenstoff im Boden hat als wichtigster terrestrischer Bestandteil des Kohlenstoffkreislaufs der Erde tiefgreifende Auswirkungen auf die Anreicherung von CO2 in der Atmosphäre und somit auf die globale Erwärmung. In den alpinen Graslandschaften des tibetischen Plateaus wird die Zersetzungsrate von organischem Kohlenstoffs im Boden durch verschiedene biotische und abiotische Faktoren gesteuert, die sich meist gleichzeitig ändern und häufig zu Gefrier- und Auftauzyklen führen. Es ist jedoch unklar, ob sich die Temperatursensitivität des Abbaus um den Gefrierpunkts von Waßer ähnlich verhält, ist wie in höheren Temperaturbereichen. Das Hauptziel dieser Dißertation besteht darin, die Auswirkungen gleichzeitiger änderungen von drei Klimafaktoren auf die Abbauraten von organischem Kohlenstoff im Boden mit Hilfe eines Inkubationsexperiments und eines biogeochemischen Modells zu untersuchen. Aufgrund der großen Divergenz zwischen empirischen und modellbasierten Ansätzen bei der Vorhersage der Auswirkungen abiotischer Faktoren auf die Bodenkohlenstoffdynamik bietet diese Dißertation zunächst einen Ansatz zur Aufdeckung einiger Unsicherheiten bei geschätzten SOC-Prozeßen in alpinen Graslandschaften. In dieser Studie habe ich die Komplexität des Modells bewertet, das erforderlich ist, um die in Inkubationßtudien beobachteten Dynamiken des Kohlenstoffs darzustellen. Informationstheoretische Metriken wie AIC und BIC sowie die mittlere Laufzeit der Kohlenstoffpartikel wurden als Kriterien für die Auswahl von Modellen verwendet, die die Daten beßer vorhersagen, ohne zusätzliche Annahmen über die Modellstruktur zu treffen. Diese Analysen zeigten, daß während des begrenzten Verlaufs eines Inkubationsexperiments der Umfang des Transfers zwischen den verschiedenen SOC-Pools vernachläßigbar ist und das Hinzufügen dieser Parameter zum Modell zu einer überparametrisierung führen könnte. Diese Ergebniße deuten darauf hin, daß Kohlenstoffmodelle mit weniger parametrisierten Strukturen, wie z. B. das Ein-Pool-Modell oder das Zwei-Pool-Modell mit paralleler Struktur, bei dem übertragungen zwischen den Pools nicht berücksichtigt werden, in der Tat eine beßere Vorhersagekraft bei der Beschreibung der Zersetzung von Kohlenstofffraktionen haben und dabei dem Grundsatz der Parsimonie folgen. Die obengenannten Informationen wurden später verwendet, um die Empfindlichkeit der SOC-Abbauraten gegenüber Veränderungen der Bodentemperatur, der Bodenfeuchtigkeit und der Sauerstoffverfügbarkeit, insbesondere bei niedrigen Temperaturen, zu bewerten. Funktionen des Dualen Arrhenius-Michaelis-Menten-Modells (DAMM) wurden in ein Ein-Pool-Modell des SOC implementiert, das als Differentialgleichung erster Ordnung mit zeitabhängigen Koeffizienten dargestellt wurde. Ein manipulativer Frost-Tau-Zyklus wurde auf einem Boden aus tibetischem Grasland angewandt, zusätzlich zu Behandlungen der Bodenfeuchtigkeit, die von extrem trocken bis vollständig gesättigt reichten, sowohl unter oxischen als auch anoxischen Bedingungen. Die intrinsischen Empfindlichkeiten deuten darauf hin, daß die Temperatur (Energie) der Hauptfaktor ist, der die Zersetzung in kalten Umgebungen einschränkt, vorausgesetzt, Feuchtigkeit und Sauerstoff sind ausreichend vorhanden. Die intrinsischen Empfindlichkeiten in Bezug auf die Bodenfeuchtigkeit und die Sauerstoffkonzentration sind jedoch nur in sehr eingeschränkten Bereichen relevant, wenn die Böden fast trocken oder teilweise anoxisch sind, und kleine Veränderungen innerhalb dieser Bereiche können zu großen Veränderungen der Zersetzungsraten führen.

Keywords

Keywords:

Soil organic carbon decomposition
Carbon dynamic modelling
Sensitivities to climate warming

Schlagwörter:

Abbau von organischem Kohlenstoff im Boden
Kohlenstoff-Dynamik Modellierung
Empfindlichkeiten gegenüber Klimaerwärmung

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Abbreviations

AIC	Akaike Information Theory
BIC	Bayesian Information Theory
DAMM	Daul Arrhenius Michaelis-Menten model
DOM	Dissolved Organic Carbon
E_a	Activation Energy
NAMORS	NamCo Monitoring and Research Station for Multi-sphere Interactions
Pg C	Petagram of Carbon
SIDb	Soil Incubation Database
SOC	Soil Organic Carbon
SOM	Soil Organic Matter
TP	Tibetan Plateau

CHAPTER 1

Introduction

1.1. General overview of the stat-of-the-art of SOC carbon and climate warming

The quantity of carbon stored in terrestrial ecosystems is the result of the balance between two major fluxes: addition of carbon through photosynthesis and removal through a variety of processes such as soil respiration, erosion and runoff, and carbon loss as dissolved carbon (Luo and Weng, 2011, Trumbore, 2006). Soil respiration in the form of CO_2 or CH_4 fluxes occurs primarily from two sources: autotrophic respiration, including respiration by roots and root-associated organisms (e.g., mycorrhizae), and heterotrophic respiration, including microbial respiration from the decomposition of soil organic matter. Both forms of respiration are temperature sensitive (Bååth and Wallander, 2003, Lloyd and Taylor, 1994). We are in a historical moment when climate warming effects are more conspicuous for humankind than at any other time. Soils are among the most important factors that can play the role as both a source or sink of CO_2 from the atmosphere. Soils store three times more carbon than the atmosphere, with a value of between 1500 to 2400 Pg C in the first 100 cm , with approximately 2000 Pg C below this depth (JingYun et al., 2010). This reservoir is three times larger than the atmospheric carbon reservoir (Friedlingstein et al., 2019). However, several decades of extensive usage of soils, coupled with other environmental factors, have changed the shape of soil profiles. The global annual C release from heterotrophic respiration is estimated at 51 Pg C yr^{-1} (Hashimoto et al., 2015), five times more than annual fossil fuel emissions, from which 10 to 30% of these current total anthropogenic emissions is only caused by land-use change (Masson-Delmotte et al., 2021).

The response of soil organic carbon (SOC) dynamics to changes in biotic and abiotic factors is a critical aspect of ecosystem responses to global change. Among the abiotic factors, soil temperature (Davidson and Janssens, 2006) and soil water content (Davidson et al., 2000, Skopp et al., 1990) are the key environmental variable responsible for the variation in soil respiration. Soil temperature as the main important abiotic factor affects the kinetics of microbial decomposition, root, and root-associated respiration. Soil moisture content controls SOC decomposition by its direct influence on enzyme and substrate diffusion in addition to affecting the sensitivity of soil temperature (Davidson et al., 2011). At the ecosystem level however, several abiotic factors covary together.

The effect of different environmental variables on decomposition has been estimated using various methods and analysis techniques. However, the effect of simultaneous changes of abiotic factors on SOC decomposition rate has not been addressed in detail yet (Sierra et al., 2015). There are several methods that can be used to study the effects of global warming on SOC dynamics, both *in situ* and under controlled conditions. Eddy covariance measurements and *in situ* soil respiration chambers can be used to measure ecosystem respiration at different spatial scales. Soil incubation approaches are powerful methods to evaluate SOC decomposition rate, especially heterotrophic respiration under laboratory-defined conditions. In these techniques, microbial decomposition rate can be directly evaluated by excluding external input to the system and eliminating the contribution from autotrophic respiration.

Data acquired from these techniques can be used for developing and testing SOC dynamic models. There are many parameters in SOC dynamic models that measuring them in the field or laboratories is not always possible. Models can be employed in estimating these parameters. Hence, there is large uncertainty in the reported data and estimations mainly due to the inconsistent source of data, from *in situ* or lab measurements. Especially, predictions have mostly focused on labile carbon with short decomposition times.

In this dissertation, I discuss soil incubation studies coupled with SOC dynamic models and the source of information that we can extract from these methods. I will explain how the interpretation of the same source of data can provide us with various understandings of the overall dynamic of SOC. I then use this information to evaluate the sensitivities of SOC decomposition rate to changes in soil temperature, soil moisture, and oxygen availability, especially at low temperatures.

1.2. Understanding SOC decomposition in the Tibetan Plateau

The Tibetan Plateau (TP), with an average elevation of 4,000 m above sea level and an extensive area covered by glacial and periglacial deposits, has been known as the **Third Pole** of the Earth (Qiu, 2008). The plateau along with the other vulnerable ecosystems, such as the Arctic, has experienced increased rates of warming. Over the past 50 years, a rise in temperature of up to 0.3°C per decade has been recorded on the Tibetan Plateau. This increase in temperature is approximately three times more than the average global rate of warming (Qiu, 2008). The rising temperature has an especially significant impact on the hydrological cycle in the Plateau including melting glaciers, thawing permafrost, rising lake levels, and increasing in wetland areas (Wang et al., 2018, Yang et al., 2011). The high spatial heterogeneity in terrain, together with constant and simultaneous variation in temperature and precipitation, has shaped the diverse ecosystems of TP (You et al., 2019).

Tibetan grasslands play an important role in regional socio-economic development by supporting the livelihood of nomadic and semi-nomadic herders. These grasslands have experienced important changes in land use with the aim of sedentarisation that leads to constructing extensive infrastructure. Tibetan grasslands, with an area around 450,000 km^2, are characterized as the Earth's largest pastoral alpine ecosystems (Miehe et al., 2019), and store nearly 4.0% of global soil carbon (6.81 Pg only in 30cm of soil) (Zhou et al., 2019). This fast development, in addition to the climate change, is affecting both ecosystem structure and the carbon cycle extensively. To date, around 30-70% of Tibetan pastures have been degraded to different degrees (Li et al., 2013), and it resulted in high uncertainty in projecting the carbon balance of Tibetan grassland under future climate change. In the other words, it is not clear whether a short but warmer vegetation period will enhance photosynthesis, stimulating net carbon uptake, or trigger increases in SOC decomposition via amplification in soil respiration.

Therefore, there is an important need to identify the main drivers of the overall carbon balance in the TP and the fate of SOC as affected by changes in climate and land use. There is a large disagreement in the magnitude of the CO_2 flux to the atmosphere in the

TP. For instance, previous studies have shown contrasting results with warmer temperatures having negative (Li et al., 2011), positive (Wan et al., 2005), or no effect (Wang et al., 2014, Zhang et al., 2015) on SOC decomposition in Tibetan pastures. Some studies have shown that the impact of climate warming on the carbon balance of alpine grasslands was not significant, which may be due to the compensation in the increased carbon emission caused by climate warming, through the enhanced net CO_2 uptake by the increased land cover across the plateau (Guan et al., 2018, Nieberding et al., 2021). In other words, the counteract increase in the rate of both processes of carbon uptake and carbon loss can balance the carbon dynamic. The lack of consistent responses of SOC to warming is not surprising, given the complexity of key controlling factors for carbon cycling in heterogeneous environments such as the TP (Zhou et al., 2013). Therefore, more information is required to predict how climate change will affect SOC in grassland ecosystems in the future.

1.3. Models of Soil Carbon Decomposition

Soil organic matter decomposition is a fundamental process within the Earth system. Through this process carbon along with other biogeochemical elements fixed by plants in the process of photosynthesis are transferred to the atmosphere and the hydrosphere in mineral form (Trumbore, 2006). This release of carbon is fundamental for other processes in the Earth system, such as the global energy balance, with important consequences for climate. The use of models to simulate and project the carbon balance has become an important tool to studying the development and changes of ecosystems (Moyano et al., 2013, Sierra et al., 2015). In most models, SOC is usually fractionated into multiple pools with homogeneous decay rates and expressed by systems of differential equations. The components of SOC pool models can be represented as vectors and matrices whose dimensions correspond to the number of state variables (Sierra et al., 2015):

$$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I} + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C}(t), \tag{1.1}$$

where the vector $\mathbf{I}$ stands for the amount of external carbon input into the system at the time t. The vector $\mathbf{C}(t)$ symbolizes the amount of carbon storage in each pool at the time of t. The matrix $\mathbf{A}$ determines the model structure, is an $m \times m$ matrix, and contains the decomposition rates in the main diagonal, and in the off-diagonals coefficients that represent transfers of carbon among pools. The function $\xi(t)$ is a time-dependent scalar function that can be obtained from multiplying additional functions that depend on environmental variables affecting decomposition and transfer rates. The importance of the function $\xi(t)$ is in representing the dependency of SOC decomposition to different environmental factors, and it can also be used to obtain the sensitivity of decomposition with respect to changes in the environemnt (Sierra et al., 2012a). The dependency of SOC decomposition rate to abiotic factors can be expressed as a mathematical expression in which decomposition rate is a function of independent abiotic variables.

Nevertheless, similar to all biochemical reactions, soil organic carbon decomposition is a temperature-dependent reaction process. It means that increases in temperature lead to increases in the decomposition rate of soil carbon. This dependency can be formulated with Arrhenius function (Sierra et al., 2012a). The separate intrinsic sensitivities of decomposition rate with respect to abiotic factors can be obtained by employing the partial derivatives of each function (Lloyd and Taylor, 1994, Sierra et al., 2012a). For instance, the intrinsic sensitivity of decomposition rate with respect to soil temperature and soil moisture calculated using the partial derivative of each function as:

$$\frac{\partial \xi}{\partial T}; \frac{\partial \xi}{\partial M} \tag{1.2}$$

Temperature sensitivity of decomposition has been also broadly defined by the coefficient Q_{10}, which is a measure of proportional change in the process of a system once temperature increases by 10 °C (Davidson and Janssens, 2006). Over the last decades, many studies have supported the temperature sensitivity of soil organic carbon decomposition with the *carbon quality temperature* hypothesis, which states: reactions with high activation energies (E_a) represents recalcitrant carbon fraction, and have higher temperature sensitivity than the reaction of substrates with low E_a, which represents labile carbon fractions (Conant et al., 2008, Davidson and Janssens, 2006, Knorr et al., 2005, Sierra et al., 2012a). Along with temperature, soil organic carbon decomposition rates are highly sensitive to the water content in the soil, since it can play a significant role in transferring the substrate in soil media. Besides, soil temperature may affect temperature sensitivity as well. Soil moisture in lower temperatures became more important as frozen soil behaves similarly as dry soil and very saturated soil in temperatures higher than 0°C became anoxic.

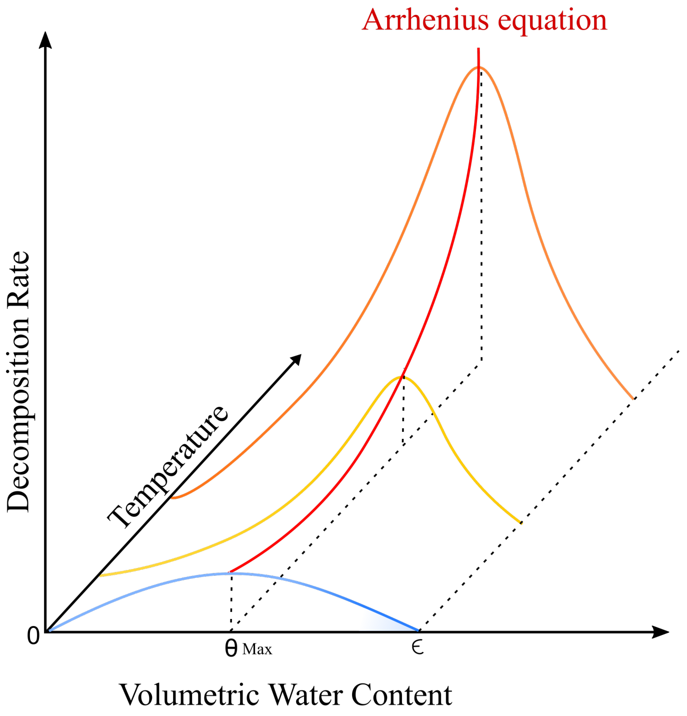

Figure 1.1.: Conceptual illustration of the dependency of decomposition rate of SOC to soil temperature and volumetric water content.

1.4. Freezing and thawing effects on SOC decomposition

The experimental approach has not clearly examined the sensitivity of SOC decomposition rate to the abiotic factors during successive freeze-thaw events. An essential issue to be addressed is the sensitivity of SOC to the simultaneous change in multiple abiotic factors, especially when they interact among themselves (Conant et al., 2011, Sierra et al., 2015).

A sharp increase in SOC decomposition is expected after each thaw, mainly due to the increase in enzyme-mediated response, especially at lower soil temperatures (Davidson and Janssens, 2006, Kirschbaum, 2006). Another explanation for this large increase is due to the lysing of microbial cells during each freezing event, resulting in more inputs to the rapidly degradable organic carbon pool (Tucker, 2014). Both mechanisms contribute to soil carbon destabilization by adding to the dissolved organic carbon pool up to 27% (Song et al., 2017), which can be taken up by microbes and metabolized. In addition, freezing and thawing cycles are accounted as an important physical disturbance that can break soil aggregates due to the expansion pressure of water in aggregates.

Assimilation of SOC by microbial communities is a frugal process in terms of energy and is limited to soluble or low molecular weight particles. Decomposition of complex particles requires more energy, which is limited at colder temperatures, hence the freeze-thaw cycle can ease the process of destabilization. Near the freezing point of water, microbial activity increases due to the availability of moisture and oxygen and is, therefore, less limited by low temperatures (Schimel and Gulledge, 1998).

In the soil saturated condition, low oxygen availability after thawing combined with increased primary productivity may lead to an increase in accumulation rate and thus increased carbon uptake. Increased freeze-thaw cycles as a result of current climate trends on the Tibetan Plateau especially during the non-growing season (Nieberding et al., 2021) could lead to larger net ecosystem respiration and potentially positive feedback to climate change.

1.5. Incubation experiments to study soil organic carbon decomposition rate

Soil incubation experiments offer a continuous observation of soil organic carbon respiration under laboratory-controlled conditions. Excluding the source of external inputs from incubated soils, provide the possibility to identify key information about the rate of carbon loss by microbial communities, the magnitude of carbon storage in different fractions, and the sole effect of any environmental variable. Soil carbon respiration is mostly monitored by measuring CO_2 and CH_4 in the headspace of incubation chambers or in the form of dissolved organic carbon in the drained soil water.

Terrestrial carbon models exploit the data from incubation experiments to predict the number of terrestrial SOM stocks under different climatic scenarios along with sensitivities of process rates with respect to changes in abiotic factors such as soil temperature, moisture, pH, etc. Depending on the duration, incubation experiments can be used to describe fractionation of soil carbon into different kinetic pools. In addition, the quality of soil organic carbon and its resistance to the external variable can be monitored. Short-term incubations (ranging from days to months) provide information on the lability of soil organic carbon, and long-term incubations (up to years) are used to study the moderate decomposable carbons or events that can accelerate the processes of destabilization in soils (Schädel et al., 2013). Observed variations of the composition of stable carbon isotopes (^{13}C) during incubation studies allow tracing carbon sources in respired carbon

(Ehleringer et al., 2000). Similarly, analyses of ^{14}C can also be used to characterize the time that carbon persists in soils.

Regardless of the plentiful application of soil incubation methods, there are disadvantages that need to be taken into account. One of the major discussions among experts in using incubation experiments is that the structure of the incubated soil is altered from that in the ecosystem; as a physical disturbance, sieving soils or removing plant debris has a major influence on the aggregated carbon particles and may affect soil carbon dynamics considerably (Six and Paustian, 2014). Additionally, the activity of the microbial community in incubations may not represent those that are active in the ecosystem. For instance, CH_4-producing microbial communities, need several months to act upon the disturbance of soils, even if their desirable environment is established (Schädel et al., 2013). This lag in their activation may result in a lower overall estimate of decomposed carbon, especially, in anoxic soils.

In periodic data acquisition from laboratory incubations, frequent monitoring at the beginning of the experiment is essential, since respiration of fast-cycling carbon dominates total carbon respired, but it declines rapidly (within days). Measurements of a fast-cycling fraction are more precise in shorted-interval measurements.

Laboratory incubations are valuable and broadly used methods to monitor the carbon decomposition in soils, but they require a set of assumptions that enable soils to be removed from their in situ context, depending on the aim of studies. These assumptions have generated methodological and interpretive disagreement among scientists. Hence, science continues to rely heavily on data from laboratory incubations to forecast future terrestrial carbon stores and fluxes. This clearly shows the need to rigorously examine laboratory incubation assumptions and their impact on the validity of incubation data.

1.6. Uncertainty in SOC modeling/models and functions

Dynamics of SOC are simulated throughout the soil profile in both local and regional levels using a number of available biogeochemical models. Almost all of these models follow a system of first-order differential equations fractionating the total SOC in three main pools. Each pool represents particles with a similar probability of being decomposed at any given time; active pools including microbial biomass and labile SOC have fast decomposition rates and carbon is decomposed within days to weeks. Slow SOM pools have an intermediate decomposition rate and are decomposed within weeks to years. Passive pools of SOC include material that can persist in the soil system for years to decades (Schmidt et al., 2011). Abiotic factors such as soil temperature, soil water availability, soil texture, land-use disturbance, and many other variables influence the rate of decomposition from these pools (Davidson et al., 2011, Lal, 2004, Sierra et al., 2015). Most SOC models include functions to estimate how changes in abiotic factors modify the decomposition rates of these pools.

There is a general lack of consensus among functions that predict decomposition rates at various levels of soil temperature and soil moisture (Sierra et al., 2015), especially in the regions with lower mean annual temperature. In cold environments such as the Tibetan Plateau water availability is highly related to the temperature fluctuation during a day. For example, studies show that in the grasslands on the Namco lake catchment, soil temperature can fluctuate between -5 at night to 25 °C in days during summer months (Nieberding et al., 2021). Soils in such grasslands can experience at least one freeze-thaw cycle per day.

1.7. Motivation and Objectives

Tibetan grasslands play a crucial role in the global budget of atmospheric trace gases, acting as a sink and/or source for CO_2. Besides, having reviewed and analyzed the state-of-the-art research in the previous sections appealed to the need to reconcile mathematical methods with incubation experiments in predicting carbon dynamics in soils especially in colder regions. In a heterogeneous environment such as Tibetan grasslands multiple biotic and abiotic factors change simultaneously and they may counteract each other. This dissertation focuses on understanding the sensitivity of SOC to the current and future scenarios in soil temperature, soil moisture, and oxygen concentration, especially in the lower temperature, where freezing-thawing events modify overall physical and chemical structures of soils and substrate availability. The importance of the freeze-thaw cycle on the SOC decomposition in these soils has not been sufficiently understood or modeled yet (Schuur et al., 2015, Sierra et al., 2015).

Nevertheless, evaluating a dynamic change in a system with interacted abiotic variables might need more adopted laboratory setups to be able to reconstruct the ecosystem environments. Soil incubation studies provide important information about the rates at which organic matter decomposes under controlled environmental conditions. Yet the apparent inconsistency in estimating the sensitivity of SOC to the abiotic factors, calls for reconsideration in using methods.

As part of this effort, in this dissertation, I aim to test different model structures using data obtained from incubation studies to determine the appropriate balance between model complexity and parsimony. I assumed that soil incubation data are not sufficient enough to get information on the rates of decompositions in all three pools of SOC in a system, mainly due to the limited observation duration. Forcing models in estimated parameters without sufficient information about the process in the system, might end with over-parameterization of a model and predicting parameters with high correlations.

In this dissertation, I use information theory metrics to select models that can better predict the data without making additional assumptions on model structure. As an additional criterion, I test estimated parameter accuracy using the concept of mean transit time.

The overall aim of this dissertation is to reconcile observed soil respiration rates in incubation approaches with soil organic carbon models for predicting the effect of warming on the process of soil carbon decomposition and microbial respiration. More specifically there are four main objectives that this dissertation attempts to achieve:

- Identify biotic and abiotic processes that are responding rapidly to climate change in the Tibetan Plateau, with a specific focus on soil organic carbon, and the exchange of carbon between terrestrial ecosystems and the atmosphere.

- Evaluate the complexity of the model that is needed to represent the dynamics of carbon observed during incubation studies.

- Predict the dependence of SOM decomposition at low temperatures, especially around the freezing point of water, at different levels of soil water content ranging from very dry to fully saturated.

- Assess the intrinsic sensitivity of soil organic carbon decomposition rates with respect to soil temperature, soil moisture, and oxygen concentration in a soil system with consecutive freeze-thaw cycles.

1.8. Overview of the manuscripts

Chapter 2/ Manuscript 1

Anslan, S., Azizi-Rad, M., Buckel, J., Echeverria Galindo, P., Kai, J., Kang, W., Keys, L., Maurischat, P., Nieberding, F., Reinosch, E., Tang, H., Tran, T. V., Wang, Y., and Schwalb, A.: Reviews and syntheses: How do abiotic and biotic processes respond to climatic variations in the Nam Co catchment (Tibetan Plateau)?, Biogeosciences, 17, 1261-1279, https://doi.org/10.5194/bg-17-1261-2020, 2020.

This chapter summarizes an interdisciplinary synthesis of current knowledge on abiotic and biotic processes affected by global warming on the Tibetan Plateau. It identifies the current state of knowledge on the influences of the modified water cycle, thawed permafrost, and degraded grasslands on the overall carbon cycle in the Tibetan Plateau.

Chapter 3/ Manuscript 2

Azizi-Rad, M., Sierra, C. A., A Model selection from incubation data for representing soil carbon dynamics. Ready for submission.

This chapter focuses on theoretical aspects of soil organic carbon studies. Using a large dataset of soil incubation studies, I test several model structures in estimating key parameters governing soil organic carbon decompositions in soil systems. I use metrics such as Akaike's and Bayes information criteria and the concept of mean transit time to evaluate the accuracy of predicted parameters.

Chapter 4/ Manuscript 3

Azizi-Rad, M., Chanca, I., Herrera-Ramírez, D., Metzler, H., and Sierra, C. A. (2021). Stochastic and deterministic interpretation of pool models. Global Change Biology, 27(11):2271-2272.

Carbon and element cycling models can be expressed in terms of the dynamics of individual particles or the collection of them in aggregated pools. Together with my co-authors, I discuss in this chapter how to interpret soil organic carbon pool models from both deterministic and stochastic points of view.

Chapter 5/ Manuscript 4

Azizi-Rad, M., Guggenberger, G., Ma, Y., and Sierra, C. A. (2022). Sensitivity of soil respiration rate with respect to temperature, moisture, and oxygen under freezing and thawing. Soil Biology and Biochemistry, 165:108488.

This chapter presents a case study on the sensitivity of soil respiration rate with respect to changes in soil temperature, moisture availability, and oxygen concentration in an alpine grassland soil in the Tibetan plateau. By employing an incubation experiment and modeling approach in a system with freezing-thawing cycles, I evaluate the key environmental variables that have dominant controls on the intrinsic sensitivity of soil organic carbon.

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CHAPTER 2

Review and syntheses: how do abiotic and biotic processes respond to climate variations in the NamCo catchment (Tibetan Plateau)

Manuscript Nr. 1

Title of the Manuscript

Reviews and syntheses: How do abiotic and biotic processes respond to climatic variations in the Nam Co catchment (Tibetan Plateau)?

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Bibliographic information

Anslan, S., Azizi-Rad, M., Buckel, J., Echeverria Galindo, P., Kai, J., Kang, W., Keys, L., Maurischat, P., Nieberding, F., Reinosch, E., Tang, H., Tran, T. V., Wang, Y., and Schwalb, A.: Reviews and syntheses: How do abiotic and biotic processes respond to climatic variations in the Nam Co catchment (Tibetan Plateau)?, Biogeosciences, 17, 1261-1279, https://doi.org/10.5194/bg-17-1261-2020, 2020.

Status

Published

Biogeosciences, 17, 1261–1279, 2020
https://doi.org/10.5194/bg-17-1261-2020

Biogeosciences
Open Access

Reviews and syntheses: How do abiotic and biotic processes respond to climatic variations in the Nam Co catchment (Tibetan Plateau)?

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Received: 5 February 2019 – Discussion started: 20 March 2019
Revised: 5 February 2020 – Accepted: 6 February 2020 – Published: 6 March 2020

Abstract. The Tibetan Plateau (TP) is the largest alpine plateau on Earth and plays an important role in global climate dynamics. On the TP, climate change is happening particularly fast, with an increase in air temperature twice the global average. The particular sensitivity of this high mountain environment allows observation and tracking of abiotic and biotic feedback mechanisms. Closed lake systems, such as Nam Co on the central TP, represent important natural laboratories for tracking past and recent climatic changes, as well as geobiological processes and interactions within their respective catchments. This review gives an interdisciplinary overview of past and modern environmental changes using Nam Co as a case study. In the catchment area, ongoing rise in air temperature forces glaciers to melt, contributing to a rise in lake level and changes in water chemistry. Some studies base their conclusions on inconsistent glacier inventories, but an ever-increasing deglaciation and thus higher water availability have persisted over the last few decades. Increasing water availability causes translocation of sediments, nutrients and dissolved organic matter to the lake, as well as higher carbon emissions to the atmosphere. The intensity of grazing has an additional and significant effect on CO_2 fluxes, with moderate grazing enhancing belowground allocation of carbon while adversely affecting the C sink potential through reduction of above-surface and subsurface biomass at higher grazing intensities. Furthermore, increasing pressure from human activities and livestock grazing are enhancing grassland degradation processes, thus shaping biodiversity patterns in the lake and catchment. The environmental signal provided by taxon-specific analysis (e.g., diatoms and ostracods) in Nam Co revealed profound climatic fluctuations between warmer–cooler and wetter–drier periods since the late

Pleistocene and an increasing input of freshwater and nutrients from the catchment in recent years. Based on the reviewed literature, we outline perspectives to further understand the effects of global warming on geodiversity and biodiversity and their interplay at Nam Co, which acts as a case study for potentially TP-level or even worldwide processes that are currently shaping high mountain areas.

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1 Introduction

The Tibetan Plateau (TP), often referred to as "The Third Pole" and "The Water Tower of East Asia", is the highest and largest alpine plateau on Earth (Qiu, 2008). With an area of about 2.5 million km^2 at an average altitude of >4000 m above sea level (a.s.l.), it includes the entire southwestern Chinese provinces of Tibet and Qinghai; parts of Gansu, Yunnan, and Sichuan; and neighboring countries (Fig. 1). The southern and eastern plateau and the adjacent Himalayas regions form the headwaters of several major rivers (i.e., Brahmaputra, Ganges, Hexi, Indus, Mekong, Salween, Yangtze, and Yellow rivers), providing freshwater for ∼ 1.65 billion people and many ecosystems in greater Asia (Cuo and Zhang, 2017). Large proportions of the inner TP are endorheic and therefore do not drain into the large river systems. On the TP, the effects of climate change are expressed more strongly than the global average, showing a steep rise in air temperature of about 0.3 °C per decade since 1960 (Yao et al., 2007) and a moderate rise in precipitation during the last few decades (Dong et al., 2018). The warming rate increases with altitude (Pepin et al., 2015), which is why the air temperature on the TP is soaring roughly twice the global average, thus substantially affecting the geodiversity and biodiversity. Glaciers and lakes are the dominant components for the Tibetan water sources, and their actual status and future development are strongly impacted by global warming. Since the 1990s, nearly all glaciers on the TP have exhibited retreat, causing a 5.5 % increase in river runoff from the Tibetan Plateau (Yao et al., 2007). The consequences of deglaciation and permafrost degradation (Wu et al., 2010) are observable in higher water and sediment fluxes, relief changes and arising natural hazards (floods, rockfalls, landslides, desertification, ecosystem degradation). Consequently, landscapes are continuously being rearranged which alters the spatial distribution and composition of the inhabiting species, many of which are endemic to the TP (Walther et al., 2002). Even conservative estimates predict substantial species extinction and considerable changes to the ecosystems (Chen et al., 2011; Bellard et al., 2012). The future trajectory of such complex processes is difficult to map accurately, thus it is important to monitor the current state as well as the evolution of this highly sensitive region. The large number of water bodies on the TP and its geological diversity, climatic setting and sensitivity to climate change make it a unique natural laboratory, which could be used as an early warning system for other alpine environments. Many lakes on the TP are superficially closed systems, which is why they are particularly suitable as "thermometers" and "rain gauges" to measure the climatic, hydrological, geomorphological, pedological and ecological changes in their respective catchments. With an area of 2018 km^2, Nam Co is the second largest lake on the central TP. Currently, Nam Co represents an endorheic system, acting as a sink for water, sediment and carbon fluxes. The existence of a former drainage ("Old Qiangtang Lake") towards northwestern Siling Co and further east down from the TP is still under discussion (Li et al., 1981; Kong et al., 2011) (see Sect. 3.1). With good accessibility and infrastructure such as the Nam Co Monitoring and Research Station for Multisphere Interactions (NAMORS), the Nam Co catchment has become a frequent study location for monitoring and tracking of environmental changes over various timescales.

Here we present an interdisciplinary overview of how Earth surface fluxes have developed with changing environmental conditions and which consequences are to be expected for biodiversity, as well as for water, sediment and carbon fluxes within the study area of the Nam Co catchment on the central TP. In particular, this review considers past and modern geobiodiversity changes with a focus on glacier retreat in relation to hydrological patterns and changes in lake water chemistry. The corresponding changes in terrestrial ecosystems concerning carbon cycle, greenhouse gas releases and pasture degradation are discussed. We provide an overview of how the paleoenvironment on the Tibetan Plateau with respect to landscape evolution around Nam Co was shaped by geodiversity, lake level changes and Holocene vegetation cover. Lastly, based on the available studies, this review identifies the major research gaps that are awaiting further exploration and comparison with other high-altitude environments.

2 Environmental changes in Nam Co and its catchment

2.1 Climatic characteristics of the Nam Co basin

The prevailing climate at Nam Co is characterized by strong seasonality, with long, cold winters and short but moist summers. During winter, the westerlies control the general circulation and lead to cold and dry weather, with daily temperature minima below −20 °C. In springtime, the TP heats up and allows the meltwater to percolate to deeper soil layers. The drought situation increases gradually until the monsoon rains arrive, typically between May and June. During autumn, weather shifts again to clear, cold and dry conditions (Yao et al., 2013). The mean annual temperature measured at the NAMORS research station (Fig. 1) between 2006 and 2017 was −0.6 °C, and the annual precipitation was between 291–568 mm (mean = 406 mm), with the majority occurring during the monsoon season from May to October

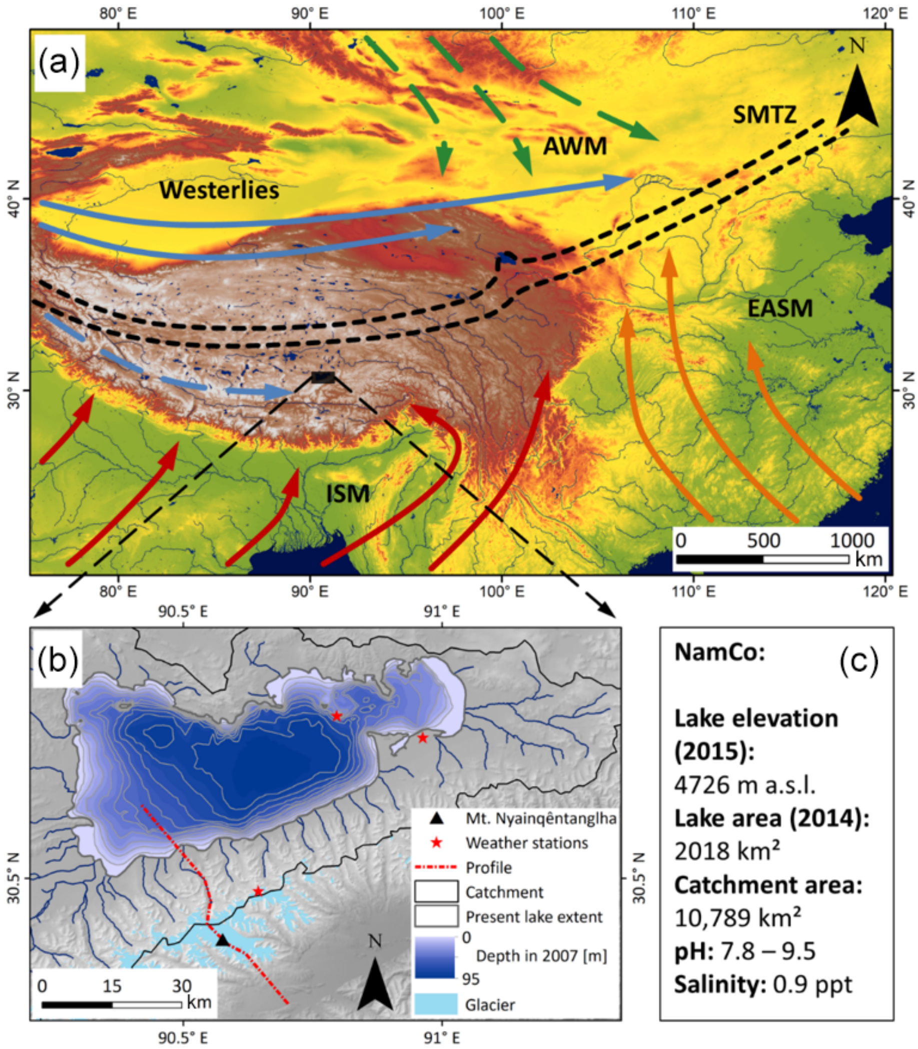

Figure 1. Major atmospheric systems governing the climate in China **(a)**. The Nam Co study site **(b)**. Characteristics of Nam Co's catchment **(c)**. **(a)** Continuous arrows indicate systems active in summer. These are the Indian Summer Monsoon (ISM) in red, the East Asian Summer Monsoon (EASM) in orange and the westerlies in blue. Dashed arrows represent systems active in winter. These are the Asian Winter Monsoon (AWM) in green and southern parts of the westerlies in blue. The dotted black lines denote the Summer Monsoon Transition Zone (SMTZ) (following Wünnemann et al., 2018). Background elevation data according to SRTM digital elevation model v4 (Jarvis et al., 2008). **(b)** Nam Co catchment, including the current lake extent (based on Copernicus Sentinel data 2018, processed by ESA), its bathymetric depth in 2007 (Wang et al., 2009a), the outline of the catchment (following Keil et al., 2010), glaciers of the Nyainqêntanglha Range (GLIMS and NSDIC 2005, updated 2018) and rivers discharging into Nam Co (SRTM digital elevation model v4; Jarvis et al., 2008). The dotted red line indicates the profile position of Fig. 2. **(c)** Characteristics of Nam Co: lake elevation (Jiang et al., 2017), lake surface area (Zhang et al., 2017), catchment area, lake pH and salinity (Keil et al., 2010).

(Table 1). The onset and strength of monsoonal precipitation varies substantially between individual years and can be delayed by up to 6 weeks, depending on the altitude and latitude on the TP (Miehe et al., 2019). Precipitation rates are subject to spatial variations due to the >7000 m high Nyainqêntanglha range, which represents the southern border of the lake catchment. This leads to considerably larger glacial areas in the southwestern area ($\sim 700\,\mathrm{km}^2$) than in the northeastern area of the mountain range ($\sim 100\,\mathrm{km}^2$) (Bolch et al., 2010).

2.2 Glacier retreat and hydrological patterns of Nam Co

The rise of satellites such as Envisat, CryoSat, and ICESat and the increasingly widespread availability of their data has enabled the accurate study of lake and glacier parameters as far back as the early 1970s (Wu and Zhu, 2008; Zhu et al., 2010b; Liao et al., 2013). The size of Nam Co and the extent and distribution of glaciers in the Nyainqêntanglha range have been the subject of many publications over the recent

Table 1. Average daily air temperature (maximum, mean and minimum in °C) and average daily precipitation (sum in mm) from NAMORS from 2006 to 2017. Calculations were performed using the tidyverse package family in R on RStudio environment (Wickham, 2017; RStudio Team, 2018; R Core Team, 2019). Data provided by ITP Beijing; for details about sensor equipment, see Ma et al. (2009).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	$\varnothing/\sum$
T_{max}	−0.7	−1.5	1.5	4.7	11.6	13.3	12.6	12.2	11.3	8.7	2.5	1.2	6.4
T_{mean}	−10.8	−9.7	−5.7	−1.4	3.1	7.9	9.1	8.3	6.5	0.3	−6.5	−8.4	−0.6
T_{min}	−21.5	−20.5	−14.3	−7.3	−4.5	1.1	5.2	3.2	−1.3	−14.7	−15.3	−19.1	−9.1
Precip.	4	1	3	13	23	41	85	117	81	34	5	1	406

years (Yao et al., 2007; Frauenfelder and Kääb, 2009; Bolch et al., 2010; Wang et al., 2013; Fig. 2; Table 1). Due to different data sources with varying resolutions as well as different mapping procedures, the estimated glacier area varies between different studies (Fig. 2; Table 1), as the delineation of debris- and snow-covered glaciers is rather subjective (Wu et al., 2016). This is especially true for the first glacier inventory (Li et al., 2003 in Bolch et al., 2010), which has been discussed in various studies due to inaccuracies and the quality of its base data (Frauenfelder and Kääb, 2009; Bolch et al., 2010). Nevertheless, recent studies show glacier shrinkage in the Nyainqêntanglha range at a rate of 0.3 %–0.5 % yr^{-1}, as measured since 1970 when the first satellite images were acquired (Fig. 2; Table 1). As a result of this glacier melting, the lake surface area has expanded from ca. 1930 km^2 to ca. 2018 km^2 at a rate of 2.1 $\text{km}^2\,\text{yr}^{-1}$ (Fig. 3a), and the lake level rose at a rate of 0.3 $\text{m}\,\text{yr}^{-1}$ until approximately 2009 and at lower rates since then (Fig. 3b). The initial rising trends of both lake level and surface area are mirrored by most lakes in the southern part of the TP, but the slowdown of this trend observed at Nam Co around 2009 seems unique (Jiang et al., 2017). This suggests that the lakes on the TP react to changing environmental parameters in a variety of different ways, and that geographical proximity among lakes does not necessarily produce similar reactions to change. The effects on freshwater input to the lake are discussed in Sect. 2.3. Although changes in monsoonal precipitation and wind direction may influence glacial retreat rates (Wang et al., 2013), rising temperatures remain their primary cause (Ji et al., 2018). The total contribution of glacial meltwater as surface runoff to this lake level increase has been estimated as ranging from 10 % to 53 % (Zhu et al., 2010b; Lei et al., 2013; Wu et al., 2014; Li and Lin, 2017), with recent studies being at the lower end of this spectrum. Increased precipitation is estimated to be responsible for 50 %–70 % of lake growth (Zhu et al., 2010b; Lei et al., 2013). Whether there is a change in evaporation remains unclear, as studies for approximately the same time period have suggested both a slightly increasing and a slightly decreasing evaporation rate since the late 1970s (Lazhu et al., 2016; Ma et al., 2016).

The rises in temperature and precipitation are also affecting permafrost soils that extend over an area of ca. 1.4 million km^2 (Yang et al., 2004) on the TP. The permafrost layers can be described as relatively warm and thin, with temperatures mostly $> -1.5\,^{\circ}\text{C}$ and < 100 m thickness (Wu et al., 2010). The mean annual soil temperature of permafrost in particular areas of the TP has increased by 0.1–0.3 °C between 1970 and 1990 (Cheng and Wu, 2007). Simulation studies have shown that due to climate warming the permafrost extent may decrease by 9 %–19 % by 2049 and by 13 %–58 % by 2099 (Li and Cheng, 1999; Nan, 2005). Although there is no clear estimate of permafrost extent in the Nam Co basin, Tian et al. (2009) reports a lower limit of permafrost at an elevation around 5300 m a.s.l. along the northern slopes of Mt. Nyainqêntanglha (7162 m). A frost lens was also encountered 9 m below the surface (4738 m a.s.l.) while sampling an outcrop along the right bank of the Gangyasang Qu close to the northwestern lake shore in 2005 (Schütt et al., 2010). Thus, due to increasing temperatures, permafrost degradation may serve as an additional recharge factor to groundwater, resulting in increased subsurface inflow into the lakes.

Focusing on Nam Co, the hydraulic interaction between lake and groundwater is still uncertain, as previous studies either neglected or ignored the influence of groundwater due to a lack of reliable data (Zhang et al., 2011). However, recent studies revealed a water imbalance, which was explained by lake water seepage with an estimated outflow of 1.9×10^9 and $1.5 \times 10^9\ \text{m}^3$ during 1980–1984 and 1995–2009, respectively (Zhou et al., 2013; Du et al., 2018).

2.3 Enhanced water availability controls changes in lake water chemistry

The maximum recorded depth of Nam Co is 122 m (Li et al., 2008a), with brackish water characterized by an alkaline pH of 7.8–9.5 and a conductivity of 1920 $\mu\text{S}\,\text{mm}^{-1}$ (Keil et al., 2010). The chemical composition of a lake is essentially a function of its climate (which affects its hydrology) and the basin geology. Increased freshwater input from precipitation, melting glaciers and thawing permafrost alters the chemical composition of the lake water and enhances surface runoff, infiltration rates and subsurface flow. Together with the input of freshwater, streams transport dissolved organic matter (DOM), which is composed of a wide range of dissolved components and particles ($\leq 0.45\ \mu\text{m}$), thus affecting the water chemistry in the lake (Spencer et al., 2014). Excessive

Table 2. Overview of glacier area changes (%) in the western Nyainqêntanglha range (changed after Wu et al., 2016).

Period	Region of the Nyainqêntanglha range	Glacier shrinkage (%)	Reference
1970–2000	Southeastern slope	−5.2	Shangguan et al. (2008)
1970–2000	Northwestern slope	−6.9	Shangguan et al. (2008)
1970–2000	Western	−5.7	Shangguan et al. (2008)
1977–2010	Western	−22.4 ± 2.9	Wang et al. (2013)
1970–2009	Western	−21.7 ± 3.4	Wu et al. (2016)
1970/80–2000	Southwestern	−19.8	Frauenfelder and Kääb (2009)
1970–2000	Nam Co basin	−15.4	Wu and Zhu (2008)
1976–2001	Nam Co basin	−6.8 ± 3.1	Bolch et al. (2010)
1976–2001	Southeastern slope	−5.8 ± 2.6	Bolch et al. (2010)
1976–2009	Detailed glaciers: Zhadang, Tangse No. 2, Lalong, Xibu, Panu	−9.9 ± 3.1	Bolch et al. (2010)

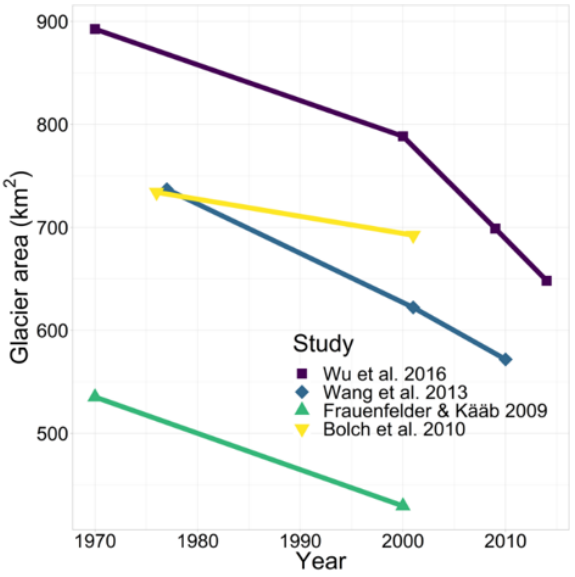

Figure 2. Glacier area reduction in the southwestern Nyainqêntanglha range since 1970 as evaluated in various studies.

landscape disturbance through removing vegetative cover causes higher rates of DOM leaching, more erosion and increasing water runoff velocity, resulting in additional input of minerals and nutrients into the lake. Since the process of DOM leaching and translocation itself is largely dependent on water and sediment cycles (Kaiser and Kalbitz, 2012), it represents both the seasonal and interannual variation in an ecosystem as well as its long-term trend. As the glaciers on the TP retreat, highly bioavailable DOM may provide additional nutrients to downstream environments and amplify the trend of eutrophication of lotic and lacustrine ecosystems. Furthermore, the rivers on the TP have been shown to transport dissolved organic carbon from thawing permafrost areas (Qu et al., 2017), which is likely rapidly degraded via microbial activity, resulting in CO_2 emissions, thus potentially producing a positive feedback on global warming. However, the research into DOM as an important allochthonous source of nutrients and as a capture of biodiversity and geodiversity of its respective catchment area is largely lacking for High Asia. The concentration and ratios of different ions in the water have a regulatory impact on the structure of biotic communities (microbes, invertebrates and fish) that can best tolerate abiotic conditions (Wrozyna et al., 2012). In Nam Co, water conductivity has been regarded as the most important environmental factor for shaping communities such as archaea, bacteria, phytoplankton, and micro-invertebrates (Hu et al., 2010; Wang et al., 2011). Studies demonstrated that ammonia-oxidizing archaea (autotrophic microorganisms) are key contributors to ammonia oxidation in deep and oligotrophic lakes (Callieri et al., 2016). This has implications for CO_2 fixation in the hypolimnion or the benthic zone, where there is insufficient irradiance to support photosynthesis, implying that archaea would perform the final step in the decay of organic matter via methanogenesis, resulting in carbon dioxide accumulation (e.g., when they decrease during winter). Although nitrification does not directly change the inventory of inorganic nitrogen in freshwater ecosystems, it constitutes the only known biological source of nitrate and as such represents a critical link between mineralization of organic N and its eventual loss as N_2 by denitrification or anaerobic ammonia oxidation to the atmosphere (Herber et al., 2020). Ultimately, the changes in the communities of primary producers could alter the lake's trophic structure, which also affects the top predators of the ecosystem. The primary productivity, as an indicator of nutrient supply and a longer growing period associated with a shorter ice cover duration, has increased markedly at Nam Co within the last 100 years (Lami et al., 2010). Wang et al. (2011) reported the increasing abundance of the diatom species *Stephanodiscus minutulus* during the last few decades (ca. 1970–2001). This species is generally viewed as an indicator of water phosphorus enrichment, suggesting increasing inputs from the lake's catchment and stronger mixing in spring season. To predict future consequences of ongoing climate change, it is essential to understand the responses of biotic communities to hydrological variations. Thus, long-term monitoring is needed to adequately address the feedbacks of recent environmental changes, while climatic conditions of the past can be reconstructed through the study of organisms such as diatoms and ostracods that are sensitive to hydrologic and chemical variations (see Sect. 3.2).

2.4 Vegetation, soils and pasture degradation in the catchment

Nam Co is located in the transitional zone between the central Tibetan *Kobresia pygmaea* pastures and the northwestern alpine steppe ecosystem (Miehe et al., 2019) (Fig. 4). Situated on the northern slope of the Nyainqêntanglha range, the vegetation pattern changes according to elevation, moisture availability and temperature. Grazing intensity and abundance of small rodents, such as the plateau pika (*Ochotona curzoniae*), may contribute to the shaping of the vegetation cover (Dorji et al., 2014; Miehe et al., 2014). The area close to the lake (< 4800 m) is covered mainly with alpine steppe vegetation consisting of *Artemisia, Stipa, Poa, Festuca* and *Carex* (Li, 2018; Nölling, 2006). Soils developed in the drier steppe areas consequentially tend to show lower organic carbon contents, naturally lowering their total C sink or source potential, as indicated by a study from Ohtsuka et al. (2008). Only one evaluable soil investigation exists from the area of Nam Co. Wang et al. (2009b) investigated two lake terrace sites, situated in the alpine steppe biome. According to their findings, the soils reflect the cold semiarid climate of the area by showing low biologic activity, while the influence of physical weathering is dominant. The soils showed several decimeter-thick layers of loess in which mainly the A horizons were developed. Although only very sparse to moderate vegetation cover occurs, an almost 30 cm thick organic-rich topsoil with granular structure was developed there (Wang et al., 2009b). Further organic-rich buried horizons were found and dated in both profiles, showing phases of climatic conditions enabling the buildup of organic material related to warm wet periods in the past (before 2.4 and 1.6 ka cal BP) and interchanging with phases of erosion, leading to, e.g., sheet erosion and the formation of gullies and alluvial fans supposedly during colder periods. These results fit well to climate reconstructions presented in Sect. 3.3 of our review. In accordance with the World Reference Base for Soil Resources (WRB) classification, we propose that the soils described by Wang et al. (2009b) can be classified as Calcisols, as there is evidence of carbonate translocation.

Higher up the slope (4800–5200 m), the alpine steppe is replaced by *Kobresia pygmea* pasture. Wang et al. (2007) and Kaiser et al. (2008) investigated the relationship between plant communities and development of soil types on the High Asian Plateau and for pasture soils in the wider area. Vegetation strongly controls the input of organic material into the soil but beyond that also stabilizes fine materials (< 0.1 mm) and governs the degree of chemical weathering. The authors found soils with stronger signs of biologic activity and chemical weathering (e.g., Cambisols) associated with alpine pasture sites. *Kobresia* root mats are usually developed in up to 40 cm thick loess layers and form a distinctive felty horizon that protects against erosion. The genesis of this felty root mat is attributed to *Kobresia pygmaea*, since this shallow-rooted, small plant allocates most of its biomass belowground and is able to reproduce vegetatively, making it well adapted to the high grazing pressure (Miehe et al., 2008). The curious dominance of *K. pygmaea* is often linked to grazing: (i) *K. pygmaea* replaces taller plants at sites where grazing pressure is increased experimentally. (ii) Several enclosures show that other grasses and shrubs increase in dominance after grazing competition ceased (Miehe et al., 2008). Hence, the felty root mat can be seen as an effect of an anthropozoogenic plagioclimax. At higher elevation (5200–5900 m), only sparse alpine vegetation associated with initial soil processes occurs (Ohtsuka et al., 2008).

Where water availability is abundant, alpine swamps with *Carex sagensis and Kobresia schoenoides* are formed, especially at source areas, along riverbanks and in waterlogged depressions, some of which can cover large areas (Li et al., 2011). Concerning soil development in alpine wetlands, the database is sparse compared to the alpine pasture and steppe biomes. It was pointed out for alpine pastures that a strong relationship exists between plant communities and (top)soil genesis. This relationship probably also holds true for alpine wetlands, with the exception that the influences of waterlogging and seasonal fluctuations and frost–melt cycles in the water table are likely to have an effect on soils. This can be expressed in terms of formation of gleyic features, frost turbations, heaves or other azonal features related to the soil-forming effects of water (Chesworth et al., 2008). It still needs to be clarified how these waterlogged areas affect the cycling and processing of organic matter and nutrients. There is no evidence of tree species, only the evergreen shrubs of *Juniperus pingii var. wilsonii*, which are mainly found on the south-facing slopes of the northern Nam Co catchment, and shrubs of *Salix* spp. in the Niyaqu Valley in the eastern lake catchment (Li, 2018). Alpine steppe is comprised of more plant species compared to pasture and marsh ecosystems, which are predominantly covered with *Carex* spp. and *Kobresia* spp. (Miehe et al., 2011b). Alpine pastures are often described as “golf-course-like” (Miehe et al., 2014) with the intention of illustrating their unique plane surface. However, small-scale structures such as thufa or hummocks are also present. The origin of these structures around Nam Co remains unclear; however, frost heave and permafrost degradation processes are seen to play a major role (Adamczyk, 2010). The landscape, generally dominated by endemic *Kobresia pygmea* sedges, harbors only a few other species (Miehe et al., 2019), but the additional microhabitats provided by thufa and hummocks enable rarer and less competitive species to settle in niches in these heterogeneous structures (Vivian-Smith, 1997). Compared to the surroundings,

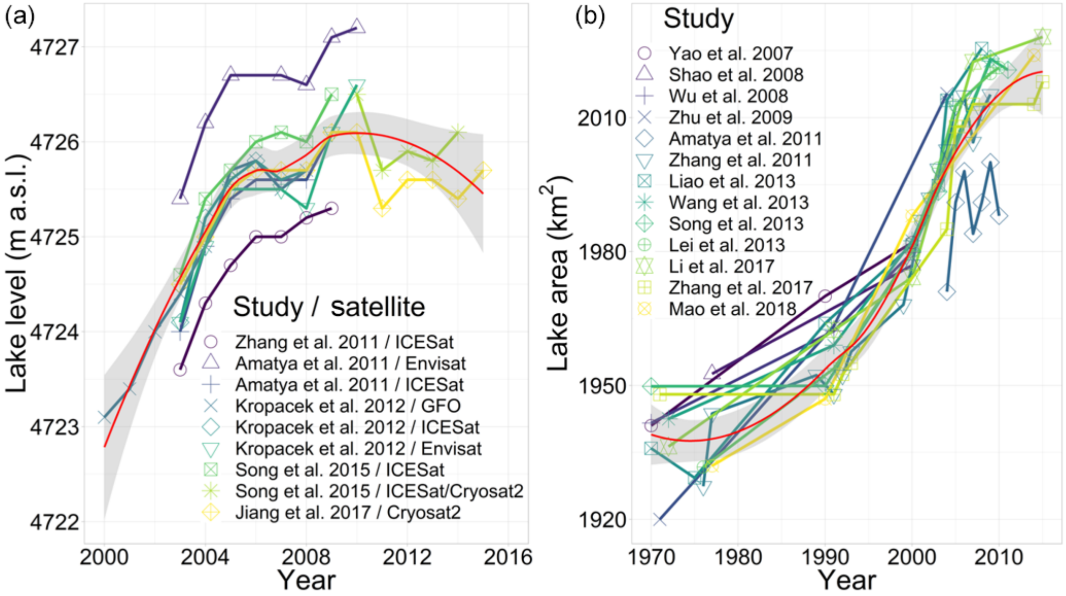

Figure 3. (a) Lake level changes of Nam Co since 2000 (there is notable shift in the water balance in 2009), and **(b)** changes of the lake surface area since 1970, as evaluated in previous studies. The overall increase rate of lake area is 2.1 km^2 yr^{-1}. Red lines denote LOESS curves, with the 95 % confidence interval shown in gray.

the microtopography of thufa possesses different degrees of wetness, exposition and insulation; depth of soil material; and type of topsoil. Local studies of the Nam Co area state that slightly degraded bare soil patches and gullies are often areas where plants have the chance to evade the suppression of the closed *Kobresia pygmea* root mat (Schlütz et al., 2007; Dorji et al., 2014). Thus, the genesis of thufa and mild, limited degradation processes are likely to increase species richness and diversity by cracking open the closed root mat of alpine pastures. These structures can also be formed by grass species that grown in tussocks (i.e., clumps, bunches or tufts), such as the endemic species *Stipa purpurea* (Liu et al., 2009) or *Kobresia tibetica* (Yu et al., 2010) and *Kobresia schoenoides* (Nölling, 2006).

The often-cited degradation of alpine pastures is likely initiated by natural polygonal cracking (Miehe et al., 2019), which can occur through drying (Velde, 1999) and then tends to be amplified by livestock trampling and plateau pikas using the cracks as highways (Liu et al., 2017b; Hopping et al., 2016). Overgrazing in alpine pastures is one of the most frequently mentioned causes of pasture degradation (Unteregelsbacher et al., 2012; Harris, 2010; Miehe et al., 2008), as excessive trampling by livestock might aggravate the initial conditions of polygonal cracking (Miehe et al., 2019). This effect, however, seems to be limited to the direct vicinity of herder's settlements and camps (piosphere centers), and many factors that are usually attributed to degradation are instead proof of environmental control, especially in drier areas (Wang et al., 2018b). Some researchers argue that climate change is the dominant or even sole driver of degradation (Wang et al., 2007), although the effects of rising temperatures and increasing precipitation appear to be an intensifier rather than the cause of degradation (Zhou et al., 2005; Harris, 2010). In turn, both Wang et al. (2018b) and Cao et al. (2019) point out that a multitude of effects might be in play, with a locally differing magnitude or even reversion, while usually moderate grazing was not found to cause degradation. Certainly there are more factors than just grazing pressure, and there might be site-specific effects leading to nonequilibrium behavior of the study object, be it pasture or steppe (Wang and Wesche, 2016). Plot-level experiments from the Nam Co area found warming to have significant effects on the shallow-rooted *Kobresia pygmaea* by reducing the number of flowers and delaying its reproductive phenology. These changes were provoked by simulating increasing precipitation by means of snow addition (Dorji et al., 2013) and also by maintaining a moderate level of grazing combined with snow addition (Dorji et al., 2018). This underlines the importance of climate forcing on the terrestrial systems in the Nam Co catchment. Grazing should not be seen as a disturbance but as an integral part of a non-steady-state but plagioclimax environment. Currently there are no estimates of the extent of degraded land at Nam Co, but the degradation of wide areas of alpine pastures is not without consequences for pastoralist communities. The severe degradation and sloughing off of the whole topsoil removes the basis for business and might lead to unknown consequences for the lake ecosystem by means of enhancing or terminating nutrient exchanges. The economic rationale of herders might be to increase the numbers of livestock, as this represents a form of social security (Simpson et al., 1994). The bottom line is that conflicts arise as less land is available for grazing (Hopping et al., 2016).

The Chinese government has favored policies such as sedentariness and fostered the construction of stationary settlements, which have, in turn, created hotspots of overgrazing (Miehe et al., 2008). In these hotspots, large portions of the topsoil are lost by erosion and denudation, leaving only an area of humic material or subsoil, thus being called "black beach" (Miehe et al., 2008) or "black-soil patch" (Liu et al., 2017a). The remaining landscapes are usually dry, poor in plant cover and prone to further degradation. Increasing areas of bare soil patches enhance evapotranspiration, causing earlier cloud cover formation, especially before noon. This may, in turn, lead to reduced radiation and temperature at the surface, thus hampering photosynthesis and consequently overall carbon sequestration (Babel et al., 2014). However, the evolution of grasslands on the TP has been accompanied by herbivore communities; thus, the plants have developed coping mechanisms to persist under continuous grazing pressure (Miehe et al., 2011a). According to the intermediate disturbance hypothesis, species diversity is higher under moderate disturbances, which suggests the positive effect of intermediate level of grazing pressure. Indeed, a plant clipping experiment to simulate grazing demonstrated that under the effect of climate warming, the grazing activities mitigated the negative effects of rising temperature by maintaining a higher number of plants (Klein et al., 2008). Many studies hold the traditional nomadic practice to be a sustainable one (Miehe et al., 2008; Babel et al., 2014; Hafner et al., 2012), but the current policy of removing pastoralist lifestyles from certain regions could potentially reduce overall species richness.

2.5 Effects on carbon cycling in alpine ecosystems

Changes in temperature and moisture have a significant effect on the biotic community structure with feedbacks on ecosystem productivity. Alpine meadows respond with increased plant productivity to warming, while productivity may be hampered in alpine steppe ecosystems (Ganjurjav et al., 2016). As soil moisture governs the community response to warming, negative effects of warming on plant productivity likely occur due to limited water availability (Ganjurjav et al., 2016). Warming was also reported to have a negative effect on plant species diversity in both alpine meadow and steppe ecosystems (Klein et al., 2008; Ganjurjav et al., 2016). Possible explanations for a decline in plant species diversity include changes in small mammal activity, storage of belowground nutrient resources and water stress and microclimate in general (soil temperature and moisture) (Ganjurjav et al., 2016; Klein et al., 2008, 2004). Thus, climate change may reduce the habitat quality for the local populations of grazers and reduce the well-being of the pastoralists by diminishing the abundance of palatable and medicinal plant groups. The changes in the plant productivity levels, as well as community changes, affect the local carbon cycle. Alpine grassland root mats on the TP are estimated to store up to 10 kg of carbon (C) per square meter (Li et al., 2008b), summing up to roughly 2.5 % of the global terrestrial carbon stocks (Wang et al., 2002). At Nam Co, the topsoils contain an almost 30 cm thick organic-rich layer (Wang et al., 2009b), thus representing considerable soil organic carbon (SOC) stocks. Due to higher plant productivity, alpine meadows in general represent a CO_2 sink; however, the interannual and seasonal uptake is highly variable (Kato et al., 2004, 2006; Gu et al., 2003). Like plant productivity, the CO_2 uptake depends on water availability and temperature, which exhibit diurnal, seasonal and annual fluctuations. The overall great importance of water availability and temperature on ecosystem–atmosphere CO_2 exchange in the central Tibetan alpine *Kobresia* meadows was demonstrated in several studies through eddy covariance measurements (Zhang et al., 2018), chamber measurements (Zhang et al., 2018; Zhao et al., 2017), decomposition of cellulose cotton strips (Ohtsuka et al., 2008) and altitudinal transplantation experiments (Zhao et al., 2018). Similarly, carbon fluxes in alpine steppe biomes are driven by precipitation and temperature on a daily to seasonal and annual timescale. The interannual flux variability follows the varying monsoonal precipitation, showing a stronger tendency towards functioning as a C sink in wetter years and as a C source in drier years (Wang et al., 2018a; Zhu et al., 2015b). Soils that develop in the drier steppe areas tend to show lower organic carbon contents, therefore lowering the total C sink and source potential (Ohtsuka et al., 2008). Although the production of plant biomass may be hampered in steppes, the ecosystem may still act as a carbon sink through microbial CO_2 fixing activities, as shown by a recent study on the TP that reported relatively high CO_2 fixation capacity (29 $\mathrm{mg\,kg^{-1}}$ soil $\mathrm{d^{-1}}$, Zhao et al., 2018). Interestingly, this study also found that alpine steppe soils demonstrated significantly higher microbial CO_2 fixation capacity compared to meadow soils (29 vs. 18 $\mathrm{mg\,kg^{-1}}$ soil $\mathrm{d^{-1}}$, respectively).

As a result of increasing precipitation and glacier runoff, wetlands in the Nam Co area are expanding, thus increasing emissions of CH_4, which is 28 times more climate active than CO_2 (IPCC, 2013). A study conducted in the alpine wetlands around Nam Co reported that CH_4 emissions have increased exponentially with increasing precipitation, especially when soil moisture exceeded 80 % (Wei et al., 2015). However, there was a large difference between swamp meadows and swamps (67 and 1444 $\mathrm{\mu g\,CH_4\,m^{-2}\,h^{-1}}$, respectively). Swamps are permanently inundated, while swamp meadows are usually seasonally inundated. Furthermore, SOC stocks are higher in swamps compared to swamp meadows (Wei et al., 2015). Large amounts of SOC in combination with anoxic conditions are the main precursors for methanogens activity, which results in increasing CH_4 emissions to the atmosphere (Kato et al., 2013). Thus, the saturated soils with high SOC content produce higher CH_4 emis-

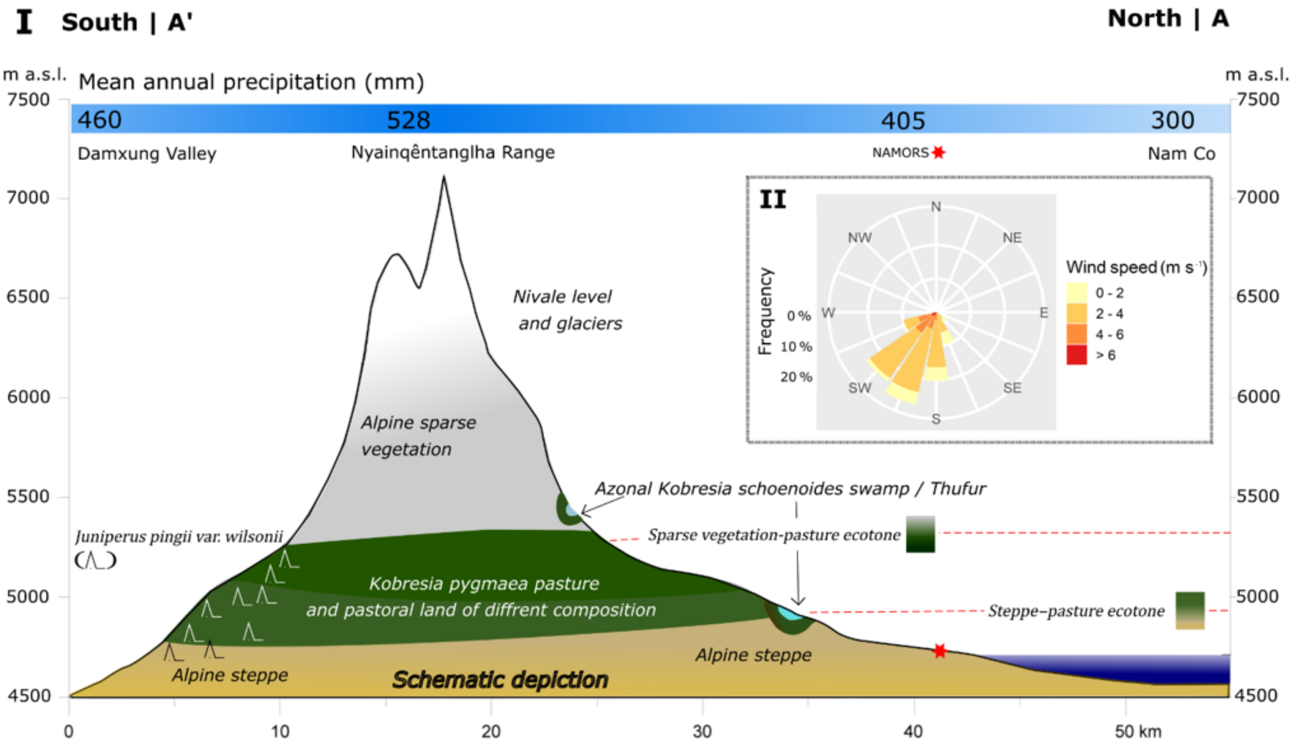

Figure 4. **(I)** Cross section from Damxung valley to the Nam Co study area (A'–A), as shown in Fig. 1b. Schematic depiction of altitude-dependent biomes and azonal landforms; changes in chroma denote height-dependent biome shifts. Approximate biome heights were gained from satellite imagery (Sentinel-2B) and herewith-derived vegetation indices, field excursions, and the literature review (Ohtsuka et al., 2008; Wang and Yi, 2011). **(II)** Frequency, direction and velocity of mean daily wind measurements at the NAMORS (30°46′22″ N, 90°57′47″ E) between 2005 and 2015.

sions (Deng et al., 2013). Observations from 2008 to 2013 at Nam Co have shown that alpine steppe and alpine meadows show annual uptake rates of 72 and 59 µg CH_4 m^{-2} h^{-1}, respectively (Wei et al., 2015); however, the corresponding emission rates are much higher. Generally, it is expected that the alpine wetland acts as a CH_4 source, while the aerated soils of alpine steppe and alpine meadow act mainly as a CH_4 sink.

As the grasslands on the TP are widely used for yak and sheep grazing, carbon cycling is influenced particularly through human activities and the degree of degradation. The intensity of grazing has a significant effect on CO_2 fluxes, with moderate grazing enhancing belowground allocation of carbon (Hafner et al., 2012), while adversely affecting the C-sink potential through reduction of aboveground and belowground biomass at higher grazing intensities (Babel et al., 2014). Overgrazing, along with the increase in burrowing pikas in the Tibetan grasslands, may increase nitrous oxide (N_2O) emissions (Zhou et al., 2018), an important greenhouse gas with 297 times larger warming potential compared to CO_2 (IPCC, 2013). Despite several studies focusing on greenhouse gas emissions on the TP, the magnitude of the N_2O emissions in different ecosystems has not yet been estimated. Experimental studies on the eastern TP demonstrated that the rate of N_2O emission may increase with increasing soil temperature and soil moisture under a future climate change scenario (Yan et al., 2018; Yingfang et al., 2018). Expanding wetland areas provide anoxic conditions for the release of methane and, due to the greater temperature sensitivity of permafrost areas, subsurface SOC is at high risk of loss, which may decrease the carbon sequestration potential in the region (Li et al., 2018). Besides carbon cycling through decomposition processes, responses to changing temperature and precipitation depend on the composition of decomposer communities (Glassman et al., 2018). Thus, the conclusive effects and feedback mechanisms (i.e., positive vs. negative loop) on warming are complex and not always clear.

3 Paleoenvironments on the Tibetan Plateau and landscape evolution at Nam Co

3.1 Geodiversity and evolution of biodiversity

Topography, geological context, climate and their complex interplay are key determinants for the distribution of organisms. In general, the ecoregion can serve as a proxy for community- and species-level biodiversity, which best describe communities of mammals, birds and plants (Smith et al., 2018). The TP forms a distinctive zoographical region, an "ecological island" (Deng et al., 2019), characterized by fauna that are adapted to high altitudes, drought, low temperatures and low oxygen levels (He et al., 2016). The TP forms unique high-altitude biogeographical biota by also harboring many unique lineages of other organisms, with a higher endemism of low dispersal species (Yang et al., 2009; Clewing et al., 2016). As mountain building has been directly associated with the development of biodiversity (Hoorn et al., 2013; Antonelli et al., 2018), the biodiversity hotspots are located in the south and southeast of the TP especially. There is also a pattern of increasing biodiversity from west to east, which correlates positively with increasing precipitation. In contrast, the harsh central areas of the TP show much lower richness but nevertheless harbor various endemics (Päckert et al., 2015). Throughout the geological formation of the TP, the mountainous southeastern parts have been hypothesized to serve as center of species diversification (Mosbrugger et al., 2018), although the core TP region is also suggested to represent a center of origin (Deng et al., 2011). The TP has been a source area for several mammalian lineages ("Out of Tibet hypothesis"; Deng et al., 2011), including the snow leopard and the arctic fox (Wang et al., 2015), as well as birds, such as redstarts (Voelker et al., 2015), and plants, such as *Gentiana* (Favre et al., 2015). These mountainous areas may also have acted as refugia, which preserved unique lineages over long periods (López-Pujol et al., 2011; Lei et al., 2014). Whether some endemic taxa represent relics of a formerly more diverse clade or have never extensively diversified remains unclear (Päckert et al., 2015). Besides being a center of origin, the TP may represent a center of accumulation as proposed by the examples of *Saxifraga* (Ebersbach et al., 2017), warblers (Johansson et al., 2007) and hynobiid salamander (Zhang et al., 2006). Overall, the regional biota of the TP is comprised mainly of Palearctic and Oriental species, Nearctic species from the Bering land bridge, as well as species from speciation in situ and postglacial recolonization from adjacent areas. The evolution of biodiversity on the TP has been affected by the combination of geological and climatic changes over the time of the uplift phases (Mosbrugger et al., 2018). Although many studies have associated recent in situ radiations to different uplift phases of the TP, Renner (2016) pointed out that the evidence for recent rapid uplift (9–8 or 3.6–2.6 Ma) remains doubtful and controversial. As proposed by the "mountain geobiodiversity" hypothesis, the evolution of biodiversity on the TP is a result of an increasing local geodiversity in combination with rapid climatic oscillations and steep ecological gradients (Mosbrugger et al., 2018).

The combination of geological, climatic and ecological changes has left its footprint in the history of Nam Co. There are at least seven different levels of continuous terraces around Nam Co, with the highest being over 30 meters above the current lake level, corresponding well with the elevation of the natural spillway in the northeast of Nam Co. Several authors claim the existence of a much larger fluvial lake system called Old Qiangtang Lake, which covered an area of around 30 000–50 000 km^2 or more (Li et al., 1981; Zhu et al., 2002). The connections provided by a large lake allowed gene flow between drainages, which is reflected, for example, by the closely related clades of schizothoracine fish (Cyprinidae, Osteichthyes) from Nam Co and the surrounding lakes, compared with more distant parts of the TP (He et al., 2016). In contrast, due to a vector-mediated passive dispersal across large areas, other aquatic taxa, such as freshwater snails, seem to have been less influenced by drainage histories (Oheimb et al., 2011). Higher lake terraces are older, suggesting a long-term reduction in lake level (Zhu et al., 2002). This may be associated with an evolution from wet to dry phase, which Li et al. (1981) connects to the gradual uplift of the plateau from early Pleistocene to the Holocene. However, there is an alternative suggestion to this interpretation of a rather modern uplift proposed by Renner (2016) who states that large parts of the TP had already reached average heights of 4000 m and more during the mid-Eocene (∼ 40 Ma ago). Recent findings of palm leave fossils on the central part of the TP, dated to ca. 25.5 ± 0.5 million years, do not suggest a presence of such a high plateau before the Neogene (Su et al., 2019). Thus, although it is suggested that the final large lake phase took place ca. 40–25 ka cal BP (Lehmkuhl et al., 2002; Zhu et al., 2002), the complex relationship between evolution of the TP and the development and the temporal existence of Old Qiangtang Lake are not completely resolved.

3.2 Holocene lake level changes and climate reconstruction based on aquatic bioindicators

Lake sediments contain important indicators or proxies that can be used to reconstruct limnological and (hydro-) climatic conditions over long time periods (Zhu et al., 2010a; Wrozyna et al., 2010). Widely used environmental indicators include communities of diatoms (Bacillariophyceae) and ostracods (Crustacea) as they are abundant and usually preserve well in sediments (Kasper et al., 2013). For example, the investigations of Quaternary ostracods, modern assemblages, and stable isotopes from Nam Co and nearby water bodies represent the most detailed application of ostracod analysis in the south–central region of the TP (Mischke, 2012). Different approaches (stratigraphy, paleoecology, etc.) detected several climatic fluctuations between warmer–cooler and wetter–drier periods (Fig. 5). In general, higher lake levels based on aquatic fauna suggest a more humid environment during the early and middle Holocene, which displayed a shift pattern compared to the northern TP (Wünnemann et al., 2018). Together with the indicator species approach and the application of transfer functions for Nam Co sediments, different stages can be recognized. In Stage I (8.4–6.8 ka cal BP), the climate changed from warm humid to cold arid with water depth being much lower than today (Zhu et al., 2010a). In Stage II (6.8–2.9 ka cal BP), environmental conditions returned to warm and humid (Zhu et al., 2010a). During 4–2 ka cal BP, lake water depth initially remained much shallower than today but then gradually increased due to high rates of precipitation (Frenzel et al., 2010). The presence of the diatom taxa *Stephanodiscus* in this stage indicates stronger monsoon activity and higher availability of nutrients (Kasper et al., 2013). Finally, in stage III (2.9 ka cal BP to present), the climate again became warm humid, with a cold dry event between 1.7 and 1.5 ka cal BP (Zhu et al., 2010a). Between 2 and 1.2 ka cal BP, benthic diatoms inferred a lower water level and drier climate (Kasper et al., 2013). Subsequently, wetter conditions and an increase in lake level was detected (1.2 ka cal BP until 250 cal BP), possibly corresponding to the Medieval Warm Period (MWP), with high planktonic diatom species and high ostracod diversity (Kasper et al., 2013). During the late Holocene, the minimum water level occurred throughout the Little Ice Age (LIA) (∼ 1490 and 1760 CE) (Frenzel et al., 2010). However, the lake level increased towards the present, which is plausibly linked to the melting of the glacier due to the current warming.

Although a large number of studies describe profound hydrological changes and general climate fluctuations, there are several uncertainties regarding taxonomy, resolution and proxy sensitivities. For example, modern ostracod data detects several morphological variations, characterized by different nodding or shell sizes, which could lead to an erroneous ecological interpretation and later, vague paleoenvironmental conclusions in relation to salinity changes (Fürstenberg et al., 2015). In paleo-studies, different sedimentation rates and uncertainties in the core chronologies also cause a lack of correspondence between signals detected by different proxies (Wang et al., 2012). For this reason, it is surrogate to understand the precise causal relationships between a complex environmental gradient (e.g., water depth, water chemistry, temperature, etc.) and the response of bioindicators. Although ecological information is still poorly known for many species, ostracod and diatom assemblages represent reliable proxies to trace the climatic history of Nam Co.

Further emphasis should be placed on combining morphology and DNA analysis to corroborate the classification of the species already described. Furthermore, experiments with living individuals should be performed under controlled environmental variables to allow the setup of a transfer function that could be used to evaluate quantitative data for paleoreconstructions.

3.3 Holocene vegetation cover and climate reconstruction based on pollen records

The comparison of modern pollen assemblages with those from sediment cores allows the reconstruction of floristic diversity and distribution across various timescales. Vegetation patterns contribute to the reconstruction of past climate and the assessment of the degree of local human influence. Modern vegetation belts around Nam Co reveal that alpine steppes contain mostly species of *Artemisia* (Asteraceae) and Poaceae, while alpine meadows and swamps are dominated by Cyperaceae (Li et al., 2011). The sedimentary pollen ratio of *Artemisia* to Cyperaceae (A/Cy) can, within certain limitations, be used to reconstruct past climates (Li et al., 2011; Li, 2018; Zhu et al., 2015a) provided that vegetation belts move with altitude during climate change. For example, when the climate is warmer and drier, alpine steppe reaches higher up the mountain, displacing alpine meadow into areas further away from the lake, leading to a higher input of *Artemisia* pollen into the nearby lake and consequently a higher A/Cy pollen ratio in the sediments. However, the A/Cy pollen ratio and abundance of tree pollen originating from a short distance can be altered by human-driven change of plant composition, hence the beginning of pastoral economy might limit the explanatory power of pollen records (Adamczyk, 2010; Miehe et al., 2014). Pollen composition inferred from sediment cores reveals a downward shift of the altitudinal vegetation belts since 8.4 ka BP (Li et al., 2011). A major extension of alpine pasture and alpine sparse vegetation closer to the lake shore during the late Holocene is corroborated by a pollen-based climate reconstruction from a peat core near Nam Co (Herrmann et al., 2010) and two other pollen records from the eastern lake shore (Adamczyk, 2010). They found a trend of increasing temperatures from the late glacial until the early Holocene, accompanied by an extension of alpine steppe, tree and shrub vegetation. Already in this period, synanthrope taxa pollen are increasing in the data used by Adamczyk (2010) with the only small occurrence of, for example, *Plantago lanceolata* in the whole profile. This very early signal shows that a lot of room still exists for studies of pollen archives around Nam Co, with much doubt still persisting at present. Climate fluctuated between dry and humid from 8.5 to 4.8 ka BP, with an intense cold regression between 8.1 to 7.8 ka BP. The onset of human activity at Nam Co is dated to 5.6 ka BP according to synanthrope taxa proxies (Li et al., 2011; Herrmann et al., 2010). Between 4.8 and 0.7 ka BP, a relatively stable climate with predominantly humid conditions developed (Fig. 5), and the vegetation pattern already showed trends of a human-made steppe biome, potentially a plagioclimax (Adamczyk, 2010). Since 0.7 ka BP, drier conditions prevailed.

Whether and to what extent the central Tibetan Plateau was forested and what caused the forest decline are the subject of ongoing discussion (Miehe et al., 2006, 2019). This matter is closely related to the prior discussed onset of more intense human activity in the area, since parts of the discussion involve a human-made forest clearing in combination with a natural forest decline. As stated, there are only occurrences of shrubs (*Juniperus pingii var. wilsonii* and *Salix*, Nölling, 2006) in the Nam Co area. No remains and no reliable evidence of a once tree-rich vegetation have yet been

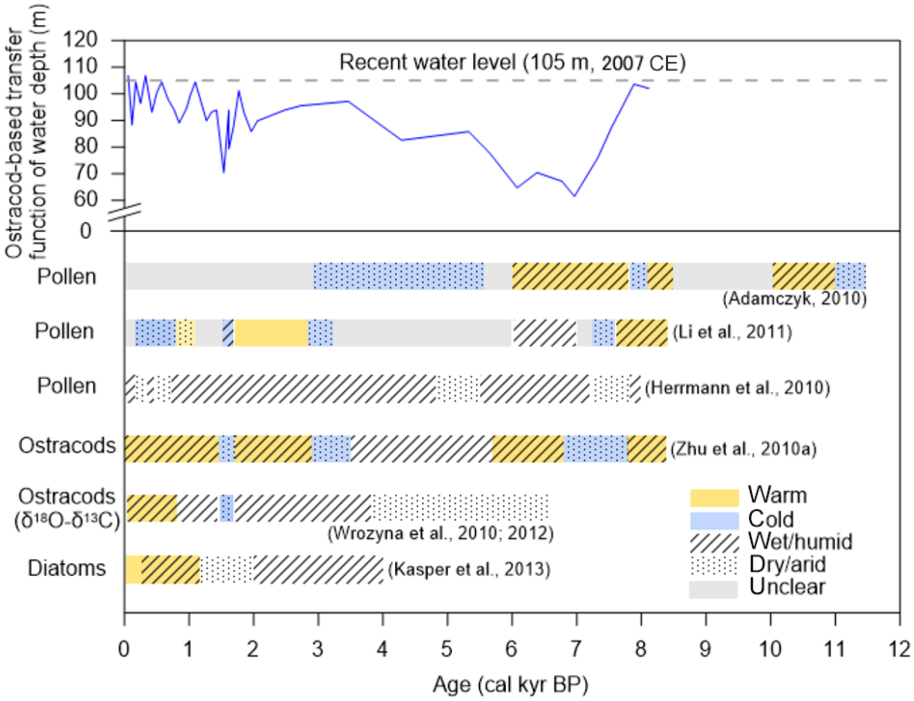

Figure 5. Comparisons of the reconstructed climate conditions based on fossils of pollen (Li et al., 2011; Adamczyk, 2010; Herrmann et al., 2010), ostracods (Zhu et al., 2010a), Ostracod δ^{18}O (Wrozyna et al., 2010, 2012) and diatoms (Kasper et al., 2013) from sediment cores in, and at the shoreline of, Nam Co. Ostracod-based water depth transfer function (Zhu et al., 2010a) (blue line) was used to indicate long-term hydrological changes and all reconstructed water depth values were adjusted to the maximum water level of the lake according to the 45 m difference between this study site (60 m) and the deepest site (105 m) at Nam Co. The main species are also shown in different periods.

found in the Nam Co catchment. According to locals, there exist several caves with potentially (pre)historic tree depictions of unknown age. Unfortunately, there is no verification of their existence nor any dating approach. Since the area of Damxung still does feature larger occurrences of *Juniperus pingii var. wilsonii* and, around 4250 m a.s.l., tree stands of *Juniperus tibetica* in enclosed areas, there is the potential to discuss that these species have been more numerous in this area in the past (i.e., last tooth theory). Miehe et al. (2019) show locations of forest relicts and give a drought line of 200–250 mm precipitation and elevations between 3600 and 4000 m a.s.l. as the upper tree line. Questions arise as to whether there has been an expansion of *J. tibetica* into the Nam Co catchment in earlier times, which would be feasible within certain limitations according to the presented thresholds. Charred micro remains as a potential sign of fire-driven forest decline are missing in one of the profiles of Adamczyk (2010) but can be found throughout the Holocene until 1 ka cal BP (Herrmann et al., 2010). The authors attribute the size and shape of the charcoal remains to local, small-scale burning of wood and leaves, not showing signs of larger forest clearings. In addition to the burning of *Juniperus* trees for religious reasons (Miehe et al., 2006), trees and shrubs may have been burned for heating or clearing of pastures by nomads. Following the presumptuous argumentation of some authors, the trees were previously able to spread again due to sufficient precipitation provided by the summer monsoon. Furthermore, the occurrence of synanthropic taxa has been observed in the nearby Damxung valley since 8.5 ka cal BP, corroborating the strong anthropogenic influence on the formation and restructuring of the vegetation patterns in the area (Schlütz et al., 2007). The decrease in summer precipitation and temperature, in conjunction with ongoing human activity, ultimately led to the total disappearance of trees and the formation of the alpine grasslands and steppe as we know them today (see Sect. 2.4). Furthermore, the occurrence of synanthropic taxa has been observed in the nearby Damxung valley since 8.5 ka cal BP (Schlütz et al., 2007). This corroborates the strong anthropogenic influence on the formation and restructuring of vegetation patterns in the area but leaves a time gap of almost 3 ka between the evidence from Damxung valley and Nam Co. Hence, further research is needed to address the question of onset of human activity and degree of landscape modification.

4 Conclusions and perspectives

This literature review summarizes the manifold environmental changes affecting abiotic and biotic processes in the area caused by past and ongoing climate change. Ecosystems on the Tibetan Plateau experience an increase in air temperature roughly twice the global average. This has accelerated deglaciation of the Nyainqêntanglha range during the last few decades, leading to substantial inflow of freshwater and various solutes resulting from weathering to the lake. The combined effects of overgrazing by livestock and warming-accelerated degradation processes of the alpine grasslands further increase surface runoff in the catchment. Moreover, warmer and wetter climate, as well as pasture degradation, may turn alpine wetlands and steppe pasture ecosystems into an overall source of methane and carbon dioxide, respectively. Based on the reviewed literature focusing on the catchment of Nam Co, we outline perspectives to improve the understanding of the close connections between geodiversity and biodiversity. (1) Permafrost areas act as buffers of the water budget and influence the behavior of geomorphological processes and periglacial landforms. Although a significant warming and consequent decay of permafrost have been reported throughout the TP in recent decades, studies on permafrost in the Nam Co catchment and in the immediate Nyainqêntanglha range are missing. (2) The rising lake level trend, starting in late 1970, had a point of reflection around 2009, which indicates changes of variable precipitation and evaporation trends, reduced water inflow from already melted glaciers, and additional ground water seepage out of the lake. Therefore, long-term monitoring is necessary to calibrate and validate models properly and to achieve a more accurate climate prognosis. (3) To improve climate modeling approaches, the dynamics of DOM, CO_2 and CH_4 fluxes need further clarification by in-depth analysis of the different biomes and in situ observations. (4) The development of molecular methods for biomonitoring and water quality assessment has advanced greatly during the last decade with the aim of providing clear monitoring standards. These offer time- and cost-effective approaches for complementary studies to tackle community shifts of various water quality indicator organisms. (5) Alongside the "traditional" paleo-bioindicator analysis, DNA-based taxa identification methods hold also a great potential for application in paleoecological studies to provide improved taxa differentiating accuracy. Various biological and geochemical proxies in Nam Co sediments have enabled the tracking of historical events and the reconstruction of past environments, which provide information about the magnitudes and directions of past climate change and thus a key to assess future changes. Both the formation of high-elevation environments and pronounced past climate oscillations have contributed to the development of biota on the TP. Interdisciplinary research of the Nam Co catchment has provided vast insights into how warming trends may affect ecosystems from microbes to the top of the food chain. Recognizing the impacts of a warming climate is the base for establishing effective climate change adaptation strategies and actions in the TP region and in alpine regions in general.

Data availability. As this paper is reviewing existing literature findings, there were no data analyzed that are not already published in the studies we cite. The dataset from which Table 1 was generated was provided by the Institute of Tibetan Plateau Research and is publicly available under https://data.tpdc.ac.cn/en/data/4deeb2b4-4fc1-4c7c-b0c6-6263a547d53f/, last access: 4 March 2020 (Wang and Wu, 2018) and https://data.tpdc.ac.cn/en/data/3767cacc-96e3-48b2-b66c-dac92800ca69/, last access: 4 March 2020 (Wang, 2019).

Author contributions. SA, MAR, JB, PEG, JK, WK, LK, PM, FN, ER, HT, TVT and YW contributed equally to the content of the paper. AS conceived the idea and was responsible for funding acquisition. SA, JB, PM and FN structured the main text body. The following authors were in charge of the corresponding sections: JB, ER, TVT – "Glacier retreat and hydrological patterns of Nam Co"; PEG, LK – "Enhanced water availability controls changes in lake water chemistry"; PM, FN – "Vegetation, soils and pasture degradation in the catchment", "Effects on carbon cycling in alpine ecosystems", and "Holocene vegetation cover and climate reconstruction based on pollen records"; SA, PEG, WK – "Geodiversity and evolution of biodiversity" and "Paleo-lake level changes and climate reconstruction". The tables and figures were prepared as follows: ER – Fig. 1; JB and FN – Tables 1 and 2 and Figs. 2 and 3; PM – Fig. 4; WK – Fig. 5.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. We thank all colleagues who contributed to this review. We especially thank Miguel Vences and Bernd Wünnemann for their enriching comments that greatly improved the manuscript. We also thank Binbin Wang for providing precipitation data. The authors are very grateful to Georg Miehe and one other anonymous reviewer for their helpful comments that greatly helped to improve the review. This research is a contribution to the International Research Training Group (GRK 2309/1) "Geo-ecosystems in transition on the Tibetan Plateau (TransTiP)" funded by Deutsche Forschungsgemeinschaft (DFG).

Financial support. This research is a contribution to the International Research Training Group (GRK 2309/1) "Geoecosystems in transition on the Tibetan Plateau (TransTiP)" funded by Deutsche Forschungsgemeinschaft (DFG).

Review statement. This paper was edited by Kirsten Thonicke and reviewed by Georg Miehe and one anonymous referee.

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CHAPTER 3

Model selection from incubation data for representing soil carbon dynamics

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Manuscript Nr. 2

Title of the Manuscript

Model selection from incubation data for representing soil carbon dynamics

Authors

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Status

Ready for submission

abstract

Soil incubation studies provide important information about the rates at which organic matter decomposes under controlled environmental conditions. These experiments offer important opportunities to parameterize soil carbon models, however there is uncertainty about the most appropriate model structure that can be obtained from incubation experiments. Here, we used time series data from 158 incubations from different soils to test different model structures and determine the appropriate balance between model complexity and parsimony. We used information theory metrics to select models that can better predict the data without making additional assumptions on model structure. In other words, we determine what model structure can be identified from the data alone without making extra assumptions of possible processes occurring during decomposition. Our results showed that soil incubation data do not provide enough information to identify rates of stabilization or destabilization usually encoded in transfer coefficients in dynamic models. The data also did not provide evidence for the existence of one single homogeneous pool that decomposes at one single rate. Instead, the analysis provided strong support for the existence of two distinct pools that decompose at identifiable rates, but without exchange of carbon among them. Our analysis also suggests that information on the time carbon stays in soils (its transit time), usually encoded in isotopic studies, can greatly improve our ability to identify appropriate dynamic models from incubation data.

3.1. Introduction

Mathematical representations of soil carbon processes are used to study complex dynamics of carbon in soils. Hence, there is considerable uncertainty about the level of information that can be extracted from empirical studies to parameterize complex soil carbon organic (SOC) models. Considering the urge for controlling CO_2 concentrations in the atmosphere, the information resulting from SOC models are increasingly used to support management-relevant recommendations as part of policy-relevant decision support systems. Therefore, the plausibility of the model outputs have moved into the focus of interest.

Plausibility describes the probability of the model predictions being correct. While the techniques of uncertainty assessments are well established, the applications of such analyses with SOC models are still in early stages. The complex dynamics in soil can be simplified and described by implementing mathematical models informed by incubation data. Olson (1963) for the first time described the energy balance and mass transfers of OC in soil by fitting a single-pool model to litterfall data.

In controlled conditions, it is always possible to study the effects of different variables on the variable of interest. Soil incubation experiments are among those methods that have several advantages and disadvantages. However, soil incubations are very useful for studying the complex system of soil in decomposing organic matter under controlled environmental factors. For instance, soil incubations can be used to determine decomposition rates of particular organic matter fractions or the entire soil, as well as the effect of abiotic variables (e.g. temperature and soil moisture) and microbial community on the rate at which SOC is cycled (Schädel et al., 2013). By removing the input of new carbon, an incubation study can provide important information on processes such as the rate of carbon and nutrient mineralization as well as the transformation rates of different types of organic matter.

A limited number of soil properties or kinetic parameters are measurable from an incubation experiment. Hence, when data and knowledge are limited, highly complex models cannot be informed from the data alone, and thus these models would need to make additional assumptions on a large number of parameters. For instance, total soil organic carbon is usually broken up into three carbon pools based on predetermined turnover times (Davidson and Janssens, 2006, Trumbore, 1997). The active pool includes all labile carbon that have a turnover time days up to weeks; the moderate carbon pool with turnover time of years to decades; and the recalcitrant pool with a turnover time of more than several decades. The contribution of each of these pools to total CO_2 flux in an incubation experiment can be obtained from the parameters (partitioning coefficients) of a SOC model. The active pool can account for up to 20 % of the total SOC pool depending on soil type, vegetation cover, or geographical region (Trumbore, 1997). During the course of an incubation study, the largest fraction of SOC considered to be in an intermediate C-pool (Haddix et al., 2011).

A major problem which might occur during fitting of the deterministic model to the incubation data is over-fitting. It means that a simpler model with less parameters can describe the observed data equally well as a more complex model containing more fitting parameters. For example, observed data during the course of a few weeks cannot give us enough information about the dynamics of the recalcitrant carbon pool of soils, and fitting a three-pool model can end in over-parameterization or non-identifiability in several parameters (Schädel et al., 2013, Sierra et al., 2015). In practice, a simpler model can provide more realistic estimation for this soil type.

In this study, we aim to extend our interpretation of incubation experiments in understanding the complexity of soil carbon dynamics, and identify our limitations in estimating model parameters. Here we performed multiple inverse modeling analysis to identify the most parsimonious model that can be fitted to the observed data without losing information due to under/over-parameterization. We hypothesized that a one-pool model could function to some extent as a null hypothesis in that it does not invoke complex mechanisms. Alternatively, two-pool models would provide evidence of more complex dynamics of SOC mineralization and imply the existence of heterogeneous SOM that decomposes at distinct rates. For this purpose, we take advantage of a large collection of incubation studies archived in the Soil Incubation Database (SIDb), which covers a variety of soil incubation studies from many different soils and controlled conditions. A comparison of the fit of a one-pool model to the fit of multiple pool models for each time series across the range of environmental conditions represented in the database will inform whether it is necessary to invoke heterogeneity in the model and thus how much complexity is captured in a sufficiently designed and measured incubation study.

3.2. Methods

In this study, we first performed an inverse parameter estimation procedure to different model structures and obtained values of the parameters for each model for each time series of CO_2 flux from SIDb. Then, using formal model selection techniques, we evaluated the performance of each model and the plausibility of the parameters that were estimated. For each time series, the best model was selected based on the lowest score gained from the AIC considering the sample size of observation. As the second criterion, we tested the best-selected model for its reliability in estimating parameters by calculating mean transit time using the parameter estimated as model output. Whenever the model failed in estimating mean transit time, we excluded that model from model selection analysis and allowed AIC to select the best model which can estimate more realistic parameters.

3.2.1. Soil Incubation Database (SIDb)

The Soil Incubation Database (SIDb) is a collection of time series data from soil incubation experiments published in the peer-reviewed literature (Schädel et al., 2020). The first version of the database includes 44 peer-revised studies with more than 600 time series of CO_2 fluxes reported as either flux rate per day or accumulated CO_2 respiration. We used 158 time series from eight publications based on our data filtering criteria including (a) selecting only time-series where CO_2 flux has been reported as the rate per day; (b) time-series with at least 10 observation points; (c) The initial amount of SOC was recorded and if necessary, enough information for converting units was available. The selected time series had an incubation duration from 10 to 600 days.

3.2.2. Model Implementation

We implemented a linear model of SOC decomposition that generalizes all carbon models expressed as systems of differential equations Sierra et al. (2012a). The model is expressed in matrix form, and the size of the vectors and matrices define the number of pools considered in specific model structures. The general structure can be expressed as

$$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I} + \mathbf{A} \cdot \mathbf{C}(t), \tag{3.1}$$

where the vector $\mathbf{I}$ stands for the amount of carbon input into the system, which in the case of incubation studies it is equal to zero ($\mathbf{I} = 0$). The vector $\mathbf{C}(t)$ symbolizes the amount of carbon storage in each pool at time of t. The matrix $\mathbf{A}$ determines the model structure, it contains the decomposition rates in the main diagonal, and in the off-diagonals the coefficients α_{ij} that represent transfers of carbon among pools.

We fitted four different structures of the general model, a one-pool model as null hypothesis and three different versions of two-pool models. In the one-pool model the vector $\mathbf{C}(t)$ is reduced into one single value and $\mathbf{A} = k$, while in the two-pool model the vector of carbon contents contains information on the size of the fast and the slow pools.

The two-pool model with parallel structure has no transfers of carbon among the pools, and its matrix can be written as

$$\mathbf{A} = \left(\begin{smallmatrix} -k_1 & 0 \\ 0 & -k_2 \end{smallmatrix} \right). \tag{3.2}$$

The series structure has only transfer of carbon, from the fast pool to the slow pool, and can be written as

$$\mathbf{A} = \left(\begin{smallmatrix} -k_1 & 0 \\ \alpha_{2,1} k_1 & -k_2 \end{smallmatrix} \right). \tag{3.3}$$

The feedback model structure considers transfers in both directions, from the fast pool to the slow one and vise versa

$$\mathbf{A} = \left(\begin{smallmatrix} -k_1 & \alpha_{1,2} k_2 \\ \alpha_{2,1} k_1 & -k_2 \end{smallmatrix} \right). \tag{3.4}$$

The models were solved using the SoilR package (Sierra et al., 2012b) and the data collected as time series of incubation experiments were optimized using the Levenberg-Marquardt algorithm implemented in the FME R package (Soetaert and Petzoldt, 2010).

In the one-pool model we used an initial value for the search algorithm of the decomposition rate as 0.5 ($k = 0.5$) and the optimization bound was set to $0 \leq k \leq 10$. For the two-pool models, parameters has set to be optimized in the ranges $0 \leq k_{1,2} < \infty$, $0 \leq \alpha_{ij} \leq 1$, and $0 \leq \gamma \leq 1$.

3.2.3. Model Selection

In this study, we applied probabilistic statistical measures to assess both the models performance on the time series datasets and the parsimony of our models. We used both Akaike and Bayesian Information Criterion (AIC and BIC, respectively) to estimate the performance of four different candidate models as the best model that can predict the soil decomposition rate in the incubation experiments. The AIC and BIC use a scoring approach based on the log-likelihood and complexity of the model and select the model based on the logarithm of maximum likelihood and number of observations in the data (Burnham and Anderson, 2004). The AIC is given by

$$\mathrm{AIC} = 2K + n \cdot \ln(\hat{\sigma}^2), \tag{3.5}$$

and the BIC by

$$\mathrm{BIC} = K \cdot \ln(n) + 2\ln(\hat{\sigma}^2), \tag{3.6}$$

where K is the number of parameters in the models, n is the number of observations and $\hat{\sigma}^2$ stands for logarithm of maximum likelihood and calculated as:

$$\hat{\sigma}^2 = (\mathrm{RSS})/n, \tag{3.7}$$

where RSS is the residual sum of squares.

Compared to the BIC, the AIC statistic penalizes complex models less, meaning that it may put more emphasis on model performance with respect to the dataset and in turn select the most complex models. Unlike the AIC, the BIC have less emphasis on model complexity, meaning that more complex models will have worse scores and in turn they will be less likely to be selected.

The limitation of these techniques is that they are based only on statistical concepts such as the goodness of fit of the model to observed data, and the number of parameters to the model. Additional information in the dataset that can be identified by a researcher could also be used to assist in model selection. For instance, the timescale of carbon cycling predicted by a model can be used as an additional criterion to determine whether certain model structure or parameterization is reasonable. Therefore, we add in our analysis an additional selection criterion, the transit time of carbon predicted by the models.

Transit time is a random variable that describes the time that carbon atoms spend in the system, from the time carbon enters a soil until its release by respiration (Bolin and Rodhe, 1973). The mean transit time for linear autonomous systems can be computed as Metzler and Sierra (2017)

$$E[T] = -\mathbf{1}\mathbf{A}^{-1}\beta \tag{3.8}$$

where $\mathbf{1}$ is a vector containing 1s, and β is a vector containing in each element the fraction of the total input that enters the system.

3.3. Results

3.3.1. Parameter estimation

The initial value of the rate of decomposition used by the optimization algorithm at the beginning of incubation had the most influence on the success in fitting the one-pool model to the data. In general, the time series with a higher decomposition rate at the beginning of the experiment, followed by an intermediate and more constant decline, cannot be fitted with a model with only one carbon pool (Figure 3.1). In these cases, the other three structures of the two-pool models were able to fit the measurements relatively well because SOC is fractionated into two compartments with distinct decomposition rates. The sharp decrease in heterotrophic respiration can be related to having stored a limited amount of labile carbon along with a higher amount of recalcitrant carbon in the system. However, in cases with a smooth decline in CO_2 release over time, the one-pool model performs better at explaining the observed data, which contains no information on separate and distinct pools (Figure 3.2).

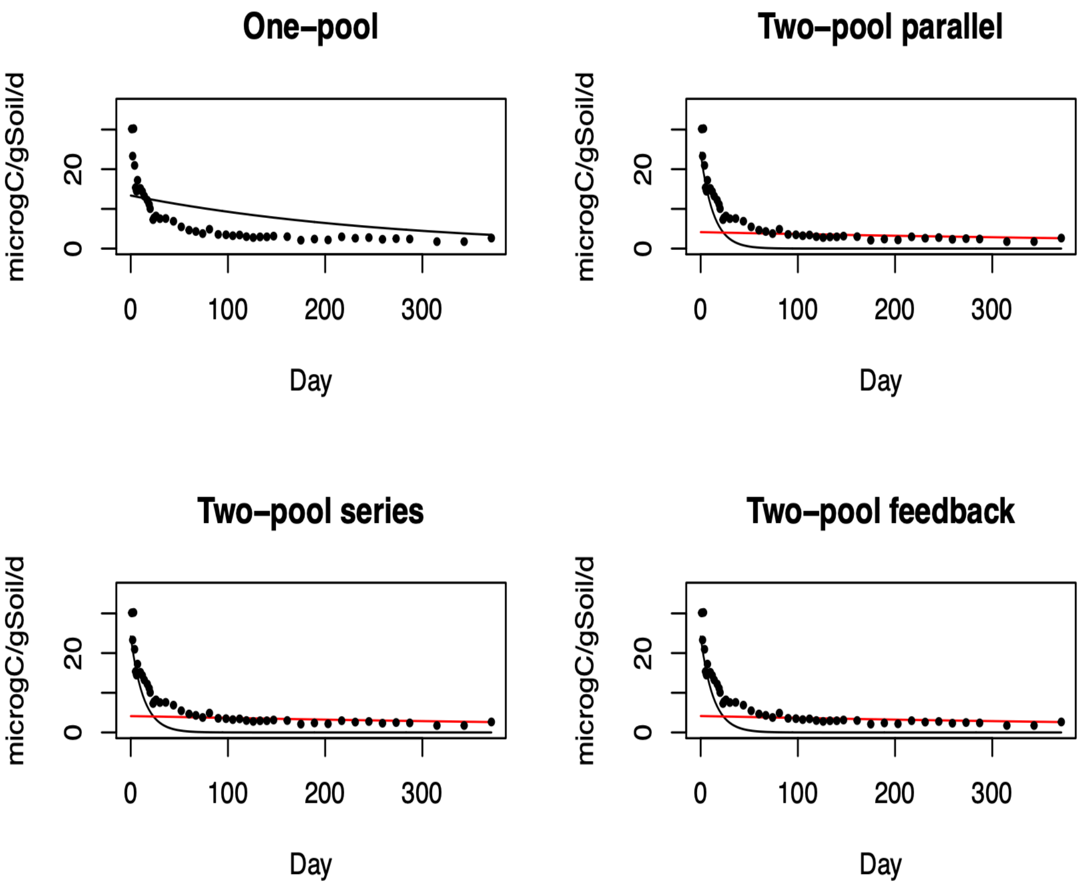

Figure 3.1.: An example for the time-series with smaller fast-pool storage. Data from Crow2019a-variable64.

In the one-pool model, which we considered as the null model, the only parameter that we needed to estimate from the model was the decomposition rate. However, in all two-pool models, there were more parameters to be estimated including (k_1 and k_2), and the

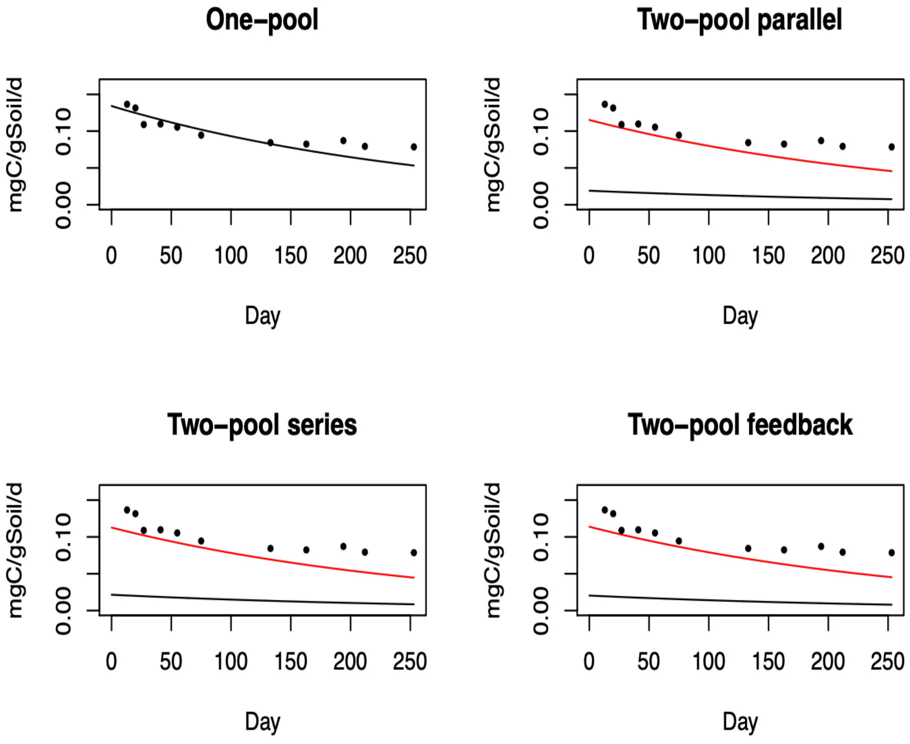

Figure 3.2.: An example for the time-series with larger fast-pool storage. Data from Ray2008-variable14.

proportional coefficient that explains how much carbon is available in each pool (γ). In addition to that, we also estimated the coefficient of carbon transfer from the fast turnover to the slow-cycling pools (α_{ij}). Our results show that in most incubation experiments, due to the short time of observations, the amount of carbon transfers between the two pools is negligible. It means a two-dimension model with two independent compartments to store carbon can explain the history of heterotrophic carbon decay regardless of the time, the number of observations, or treatment.

3.3.2. Best model selection

The results of AIC scoring showed that the two-pool model with parallel structure was selected as the best model in 66.2 % from all time series analyzed (105 times among 158 time series), while the one-pool model was selected as the best model in 22.3 % of the cases (35 times). The two-pool model in series and the two-pool model with feedback structure were selected as the best model in very few cases (11 and 7 of the time series, respectively). This means that in terms of incubation experimental data a two-pool model with an independent compartment can be used to estimate the dynamic of carbon in the system without losing information due to over-parametrization.

3.4. Discussion

3.4.1. Levels of model complexity from incubation data

SOC models are important to integrate with different sources of information and predict rates of organic matter decomposition in soils (Manzoni and Porporato, 2009, Paustian et al., 1997). The inclusion of soil processes in Earth system models has improved predictions of carbon fluxes and transfers among various reservoirs, but there is relatively large uncertainty in predictions among models (Todd-Brown et al., 2013). Existing complex models need to be tested using an integrated framework to determine what level of complexity a model can support given the available data.

Although SOM decomposition is very complex and includes various processes, it can be simulated relatively simply by using first-order decay functions (Jenkinson et al., 1990, Sierra et al., 2015), most SOC models include a large number of parameters. Obtaining parameter values for these complex models is challenging given the restricted number of measured data in incubation studies (Schädel et al., 2013, Sierra et al., 2015). Incubation

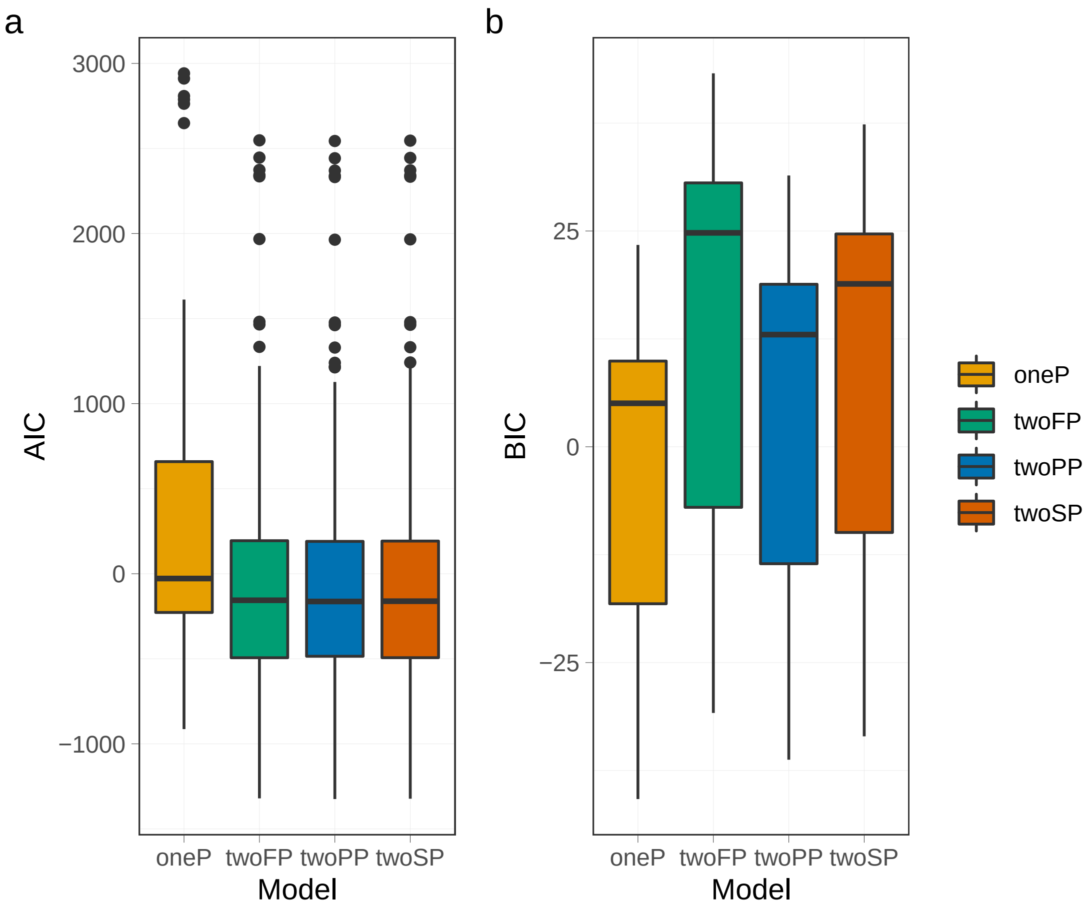

Figure 3.3.: The results of a) AIC scoring on each model considering the sample size; b) BIC scoring; The lower the values of AIC and BIC are, the better the model is; each model has been represented in one color.

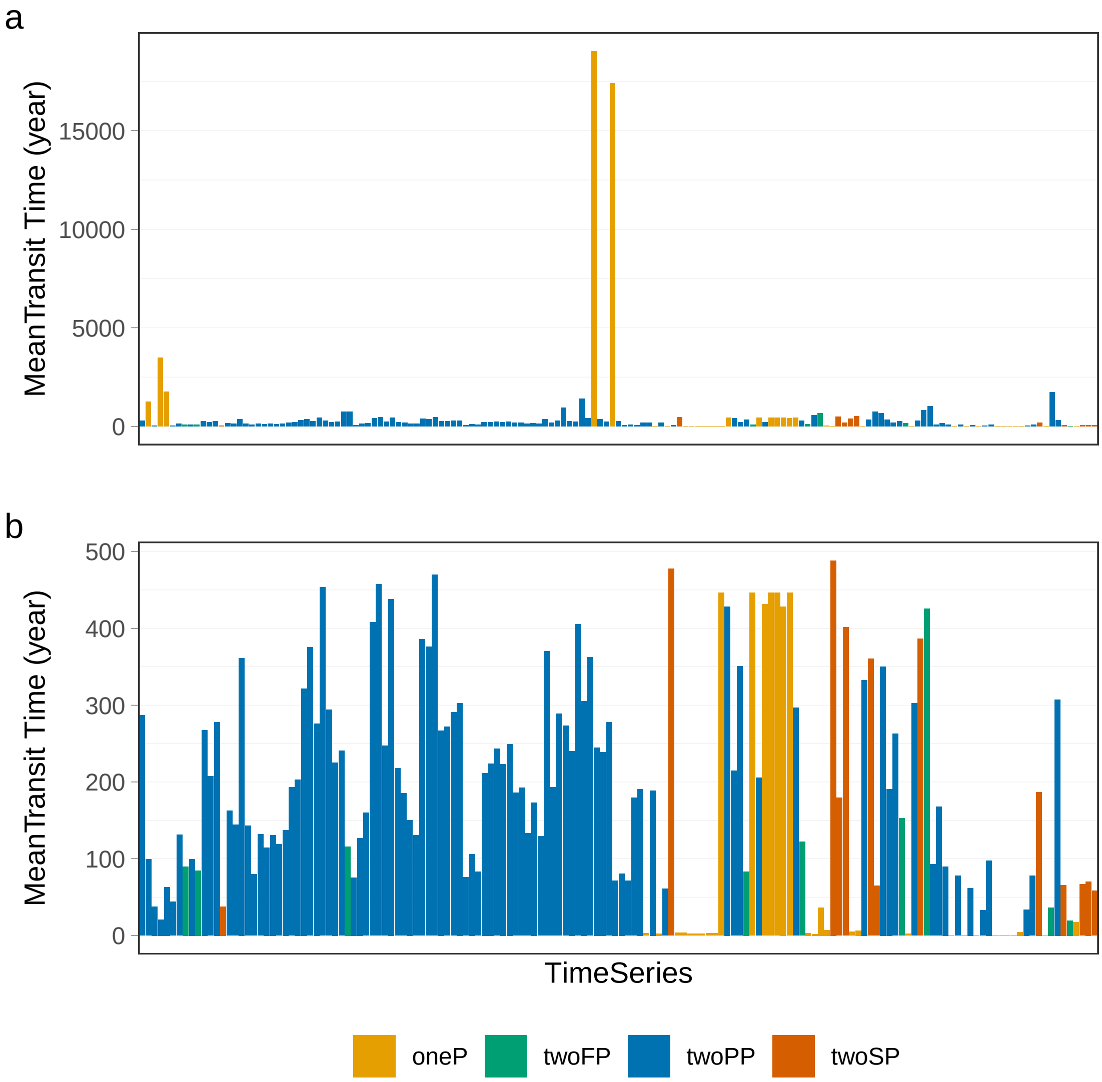

Figure 3.4.: Mean transit time of the best model selected; a) is when there is no selection based on transit time and b) selected models after limiting transit time to 500 years; Each plotted bin represent one time series. Each model structure showed in a color.

experiments are a popular approach to measure the rate of heterotrophic respiration under various biotic and abiotic scenarios and to employ this information in the process of developing or testing SOC models. In this study, we used inverse modeling implementing several model structures with the aim to estimate the key indices governing the process of SOC dynamics. We assessed the level of information that can be extracted from incubation experiments without adding extra information not supported by the observed data.

Total SOC storage measured in an incubated soil can be fractionated in two or more pools based on changes in the rate of decomposition over time. However, during the limited course of incubation experiments, not more than two fractions of SOC can be identified. For instance, in the longest time series we tested with 600 days of incubation, no more than two fractions were possible to identify. However, in a number of time series assessed, the two fractions of carbon were superfluous and only one single fraction for the bulk soil was identifiable. The number of observations also has a significant effect on the accuracy of the fractionated carbon, especially at the beginning of the experiment where we expect a fast decomposition rate of labile carbon. The fractions with a fast decomposition rate can be depleted in a range of days (Schmidt et al., 2011), and in a prolonged measurement, valuable information about this fraction of SOC can be lost.

The two-pool models with series and feedback structures include parameters of the amount of carbon that can be transferred among defined fractions of soils. While such models have been already implemented from incubation data, it is not clear whether such models follow the principle of parsimony with respect to the information contained in the data. Our analysis showed that during the short course of an incubation experiment, the levels of transfer among various pools of SOC is negligible, and adding these parameters to the model might lead to over-parameterization. Comparing the AIC scores among three structures of the two-pool model, the two pool model with parallel structure, which does not account for any transfers among pools, showed a better predictive ability in describing the decomposition of carbon fractions, while following the principle of parsimony.

This study has focussed on assessing whether a complex model is needed to map the dynamics of carbon observed during incubation studies or whether a simple model should receive priority for the sake of parsimony. A goodness-of-fit of one model solely can be assessed by looking at the root mean square errors or other metrics that measure the ability of the model to predict well some observed data. However, the AIC and BIC scores reward models that achieve a high goodness-of-fit score and penalize them if they become overly complex. They might select the simplest model only due to its simplicity and not necessarily account for the plausibility of estimated parameters.

3.4.2. Application of Finding

In the SOC models, the mean transit time of carbon particles can be applied as an additional criterion in model selection. This can be especially relevant when there is a model with a minimum number of parameters being fitted to the small datasets. Even though the selected model is the most parsimonious model with the highest goodness-of-fit among the others, the estimated parameters might have a long-distance with reality in terms of accuracy or precision. Therefore, we evaluated each model for their accuracy of parameter estimation by obtaining mean transit time from optimized parameters by each model structure. In our analysis, the one-pool model was selected as the best model based on both AIC and BIC scores, hence the estimated mean transit time by this model in most cases was in the range of hundreds of years. In this case, a two-parallel model will provide a more realistic value in terms of mean transit time, especially regarding the fast turnover carbon pool in the systems.

Our findings emphasize the implication of different criteria in model selection performance. The knowledge on the timescale that carbon resides in soil, and tracing that in both carbon stock and respired carbon can be used as an indicator to perform fractionation when modeling SOC dynamics. This knowledge at the same time can be used as a criterion to test the uncertainty in model performance, even though the model has been selected as the best model in a model selection analysis. Therefore, we see great potential for using radiocarbon information in incubation experiments to assist in the model selection process. Radiocarbon provides extra information on the time that carbon atoms have remained in the soil or in the soil respiration flux. The mean transit time of carbon predicted from a model can therefore be compared with the radiocarbon values of respired CO_2 from incubation and be used as an additional constraint to select the best model.

Knowledge on the timescale that carbon resides in soils is necessary to model how much of the total soil carbon stock is labile and respired back to the atmosphere.

3.5. Conclusion

Using a large dataset of soil incubation studies, we were able to determine that two-pool models with parallel structures offer the best compromise between model complexity and parsimony. These types of models assume two distinct phases during the course of organic matter decomposition, which corresponds to two distinct soil fractions decomposing at different rates. Therefore, incubation methods can be used reliably to fractionate SOC into two distinct dynamic fractions.

Our analysis suggests that incubation studies are generally too short to identify transfers and transformations of SOC included as transfer coefficients in the series- and feedback-model structures. Similarly, we found little evidence to represent SOC decomposition as one single homogeneous pool with one single decomposition rate.

Information theory metrics such as the AIC and BIC can help researchers to determine the most appropriate model that can be extracted from the information in the data alone without making additional assumptions. Nevertheless, we found that in some cases, the selected models provide unreasonable estimates of mean transit times, suggesting that incubation studies should be combined with isotopic studies, and in particular radiocarbon, to better determine the most appropriate model to describe decomposition in soils.

Acknowledgements

This study was developed as part of the International Research Training Group (GRK 2309/1) Geo-ecosystems in transition on the Tibetan Plateau (TransTiP) funded by the Deutsche Forschungsgemeinschaft (DFG). Additional funding was provided by the Max Planck Society.

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CHAPTER 4

Stochastic and deterministic interpretation of pool models

Manuscript Nr. 3

Title of the Manuscript

Stochastic and deterministic interpretation of pool models

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Bibliographic information

Azizi-Rad, M., Chanca, I., Herrera-Ramírez, D., Metzler, H., and Sierra, C. A. (2021). Stochastic and deterministic interpretation of pool models. Global Change Biology, 27(11):2271-2272.

Status

Published

Received: 19 January 2021 | Accepted: 25 February 2021

DOI: 10.1111/gcb.15581

Global Change Biology WILEY

LETTER TO THE EDITOR

Stochastic and deterministic interpretation of pool models

Waring et al. (2020) discuss several perceived limitations of pool models for representing soil organic carbon (SOC) dynamics and propose an approach (PROMISE) to overcome these limitations. We think it is important to critically analyze current SOC models and discuss their limitations, but we are concerned about important misconceptions and misunderstandings in Waring et al.'s (2020) contribution. Here, we would like to (1) show that pool models can display the set of behaviors that the authors say they cannot, and (2) show that the new proposed framework by the authors is also a pool model.

We treat here pool models as synonyms of compartmental models, which are mathematical models that describe how the mass inside a set of compartments or pools change over time given some starting values. To be realistic, these models must obey the principle of mass conservation in the sense that matter cannot be spontaneously created or destroyed, and changes according to the balance between inputs and outputs of mass.

1 | POOL MODELS FROM THE DETERMINISTIC AND THE STOCHASTIC PERSPECTIVE

Pool models can be studied from a deterministic or a stochastic point of view. The most common representation is through systems of first-order differential equations, which is a deterministic representation of the changes in the total amount of mass. However, compartmental systems can also be studied from a stochastic point of view, in which the dynamics of small particles or atoms are tracked and the overall system dynamics emerge from the individual dynamics of the particles (Anderson et al., 1977; Metzler & Sierra, 2018). Mathematically, they can make the same predictions for the total amount of mass and how it is distributed among the compartments, but one can also make inferences about the individual particles in the stochastic approach. Traditional pool models, such as Century with assigned values for the rates of each individual compartment, can produce distributions of the ages of particles inside the compartments, and distributions of the transit time of the particles as they travel from the input to the output flux (Sierra et al., 2018). For instance, using the original parameter values reported for Century (Parton et al., 1987), we obtained values of the age of carbon in the active pool that range from 0.06 to 13.6 year (5 to 95% quantiles of the pool age distribution), and between 13.1 and 455.6 year for the passive soil carbon pool, even though the pools are defined by constant values of decomposition rates of 3.7 and 0.006 year^{-1}, respectively. From the perspective of a particle that travels through the whole network of compartments, we predict a range of transit times between 0.007 and 13.8 year. Additional details about these computations are provided in a supplementary document.

Notice that this pool model can make the same type of predictions that the PROMISE model reports. Our example is for a system in equilibrium, but the same stochastic consideration can be done for systems out of equilibrium that evolve over time (Metzler et al., 2018). The issue is not on the model structure and the need for a new conceptual framework. Existing theoretical frameworks can already provide the type of predictions that Waring et al. (2020) advocate.

2 | ARE ALL SOC MODELS POOL MODELS?

Yes, all models that represent the dynamics of some mass in a particular system must store this mass in one or many state variables that account for its change through a mass balance. We usually call this state variable a pool, or a compartment, or give it a more specific name. But because of the mass balance consideration, its representation must follow very strict mathematical constraints, which result in the type of dynamical systems that we call compartmental systems. Even models that are described by partial differential equations can be expressed as compartmental systems after an appropriate discretization (Metzler et al., 2020).

The new framework proposed by Waring et al. (2020) is also based on a set of state variables defined according to the type of chemical compound and its location in soil pore classes. Particles are tracked by cohorts instead of aggregated masses, but they must belong to any of the predefined state variables, and move according to predefined probabilities. Table 2b in their article shows a matrix-like arrangement of these probabilities, which is analogous to how the same information is stored in a compartmental matrix (Metzler & Sierra, 2018). In other words, PROMISE is not a novel conceptual framework, it is a pool model approached from a stochastic perspective.

Nevertheless, we think that the stochastic perspective can help us to resolve controversies around pool models. It brings new insights to complex dynamical processes and opens new research opportunities to combine stochastic theory with existing compartmental models. We hope more research is done in this direction, taking advantage of the dual interpretation of compartmental

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This article is a Letter to the Editor about the article by Waring et al., 26, 6631–6643. See also Response to this letter by Waring et al., 27, e11–e12.

systems both as deterministic and stochastic. Furthermore, we hope there is a growing understanding about what current models and frameworks can do before truly novel advances can be made in SOC research.

ACKNOWLEDGMENTS

This manuscript emerged from discussions among laboratory members. All the authors contributed equally to this work, and authorship is presented in an alphabetical order. Funding was provided by the Max Planck Society and the German Research Foundation (SI 1953/2-2)

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

FUNDING INFORMATION

Deutsche Forschungsgemeinschaft, Grant/Award Number: SI 1953/2-2; Max Planck Society

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

CHAPTER 5

Sensitivity of soil respiration rate with respect to temperature, moisture and oxygen under freezing and thawing

Manuscript Nr. 4

Title of the Manuscript

Sensitivity of soil respiration rate with respect to temperature, moisture and oxygen under freezing and thawing

Authors

Azizi-Rad, M., Guggenberger, G., Ma, Y., and Sierra, C. A.

Bibliographic information

Azizi-Rad, M., Guggenberger, G., Ma, Y., and Sierra, C. A. (2022). Sensitivity of soil respiration rate with respect to temperature, moisture and oxygen under freezing and thawing. Soil Biology and Biochemistry, 165:108488.

Status

Published

Soil Biology and Biochemistry 165 (2022) 108488

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Sensitivity of soil respiration rate with respect to temperature, moisture and oxygen under freezing and thawing[☆]

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ARTICLE INFO

Keywords:
Soil carbon
Decomposition rate
Intrinsic sensitivity
Soil incubation
Michaelis-Menten
Tibetan Plateau

ABSTRACT

In alpine environments, the decomposition rate of soil organic carbon (SOC) is controlled by several biotic and abiotic factors, which mostly change simultaneously and often lead to freezing and thawing cycles. However, it is highly uncertain whether the temperature sensitivity of decomposition around the freezing point of water is similar as in higher temperature ranges. In this study, we conducted a full factorial incubation experiment using soil samples from a grassland site in the Tibetan Plateau. A manipulative freeze-thaw cycle was imposed to these soils by continuously changing temperature, from −5 to 10 °C. Additional treatments included 4 levels of soil moisture at 15, 30, 60 and 90% of water-filled pore space (WFPS), and two levels of O_2 concentration at 0 and 20%. We fitted the Arrhenius equation into the flux data to estimate the activation energy (E_a) and base flux rate (A) for each treatment level. Then, we predicted the dependence and sensitivity of decomposition rate (k) by implementing the Dual Arrhenius and Michaelis-Menten (DAMM) model using a Bayesian optimization approach. While soil temperature had the strongest control on SOC decomposition rate at all soil moisture and O_2 levels, its intrinsic temperature sensitivity ($\Delta k/\Delta T$) remained nearly constant across the entire temperature range except around 0 °C. We found that E_a was higher in nearly dry or anoxic conditions, suggesting that in these extremes more energy is required for microbial activity to take place. These intrinsic sensitivities revealed that temperature (energy) is the main factor that limits decomposition in cold environments provided that moisture and oxygen are sufficiently available. Intrinsic sensitivities with respect to soil moisture and oxygen concentration were only relevant at very narrow ranges, when soils were almost dry or partially anoxic, and small changes within these narrow ranges may lead to very strong changes in decomposition rates.

1. Introduction

Soil temperature, soil moisture and oxygen concentration are among the most important variables that influence the rate of soil organic carbon (SOC) decomposition and its sensitivity to environmental change (Singh and Gupta, 1977; Davidson et al., 2011; Moyano et al., 2013; Sierra et al., 2015). The temperature sensitivity of SOC decomposition rate at low temperatures, particularly around the freezing point of water, is still poorly understood (Sierra et al., 2015) because of difficulties in conducting experiments with several interacting variables. Furthermore, it is highly uncertain how the rate of soil respiration reacts when several environmental factors change simultaneously in addition to temperature changes alone.

In cold climates, temperature not only controls the rate of microbial activity, but also physically modifies other abiotic factors such as the availability of water for biological processes due to freezing. For instance, in the alpine grasslands of the Tibetan Plateau, large temporal variation in soil respiration is often observed, especially in the non-growing season (Wu, 2020), which can be explained by the complex interaction between temperature and soil moisture (Reichstein et al., 2003). Basically, temperature governs the rate of SOC decomposition either directly through fast substrate utilization of the unique soil

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[☆] This study was developed as part of the International Research Training Group (GRK 2309/1) Geo-ecosystems in transition on the Tibetan Plateau (TransTiP) funded by the Deutsche Forschungsgemeinschaft (DFG).

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https://doi.org/10.1016/j.soilbio.2021.108488
Received 28 May 2021; Received in revised form 22 September 2021; Accepted 24 September 2021

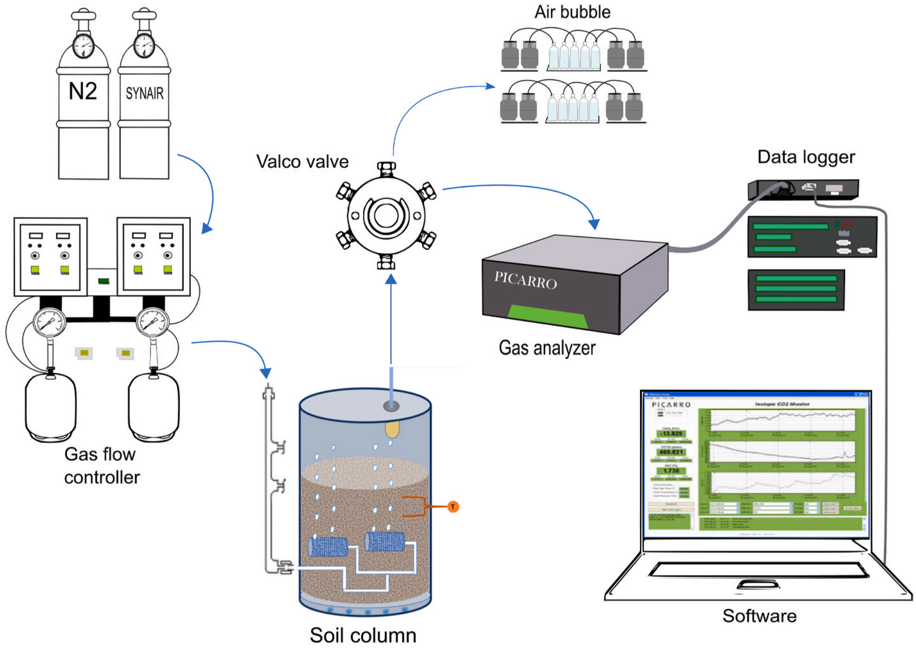

Fig. 1. Schematic diagram of the open-soil incubation setup. Blue arrows indicate the path of air from two gas cylinders with flow regulated by a mass flow controller (MFC) through the soil column to the Picarro G2301 gas analyzer. The selection of the specific soil columns for measurements was done via a Valco valve. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

microbial communities adapted to the cold temperature (Monson et al., 2006), or by indirect impacts on the diffusion of extracellular enzymes and substrates through modification of soil physical factors (Mikan et al., 2002). Despite the fact that soil respiration is lower at low temperatures, many studies have shown that SOC decomposition rate has higher temperature response in the non-growing season (defined by the Q_{10} coefficient) than the growing season (Wang et al., 2014; Monson et al., 2006). Furthermore, some studies showed larger temperature sensitivity once soil moisture becomes unavailable due to freezing in temperatures below 0 °C (Mikan et al., 2002; Tilston et al., 2010; Schmidt et al., 2008). The presence of frozen water strongly affects substrate supply, soil microbial activity, and temperature dependence of the non-growing season soil respiration (Tucker and Reed, 2016).

In alpine-cold areas, soils are predominantly exposed to large fluctuations in solar radiation and air temperatures that often lead to freeze-thaw cycles (Brooks et al., 1997). Soil freezing removes soil moisture from the liquid phase and reduces air-filled pore space due to ice volume expansion. Once temperature increases, liquid water is available again for biological activity. However, melted water could also decrease soil's aerobic conditions depending on topography. In flat or concave areas, melting of frozen soil water or snow can cause saturated-anaerobic conditions (Mohammed et al., 2019).

The Tibetan alpine grasslands, similarly to arctic tundra, are vulnerable regions due to climate warming, but the unique climate in the Tibetan plateau may expose SOC to particular cycles of freezing and thawing. The long non-growing season in this region is recognized as a cold-dry winter, receiving less than 15% of annual precipitation, therefore compared to the arctic tundra, the soils of Tibetan grasslands are less covered by snow and are much more exposed to fluctuations in solar radiation and air temperature. During the non-growing season, soils in Tibetan grasslands are usually frozen, while the daily range of surface soil temperature is large. The maximum surface soil temperature is higher than 0 °C during the day due to the absence of a persistent snowpack (Monson et al., 2006). Soil microbial processes at low temperatures are of special importance in this context, because the relative temperature sensitivity of decomposition is usually high at low temperatures (Fang and Moncrieff, 2001). The contribution of soil respiration during the non-growing season is therefore of relevance at the annual scale and should not be neglected in the overall carbon balance.

The effect of simultaneous changes in temperature, moisture, and oxygen concentration on SOC decomposition rate is captured by the conceptual framework of the Dual-Arrhenius and Michaelis-Menten (DAMM) model (Davidson et al., 2011). This model integrates well mechanistic understanding of the temperature effects in reaction rates, with constraints imposed by solubility of substrates and oxygen availability for microbial activity. The model has been successfully applied to predict soil respiration rates in well aerated soils and at high temperatures, but it has not been tested under changing environmental conditions at low temperatures such as those imposed during freeze-thaw cycles. Here we used a modified version of the DAMM model (Sierra et al., 2017) that considers temperature, soil moisture, and O_2 concentration as the main drivers of SOC metabolisms at the reaction sites where heterotrophic decomposition takes place.

With the aim to improve our predictive understanding of the mechanistic controls of SOC decomposition under changing environmental conditions imposed during freeze-thaw cycles, we addressed three main questions in this study: 1) How does the interaction between soil temperature, moisture and oxygen affect soil respiration rate during freeze-thaw cycles? 2) How does the interaction between moisture and oxygen lead to different temperature dependencies for microbial respiration rates? 3) How does the sensitivity of respiration rate differs for independent and simultaneous changes in temperature, moisture and oxygen? We addressed these questions by conducting a full factorial incubation experiment using soils from a high elevation grasslands from the Tibetan plateau, and applying the DAMM model to compute sensitivities of respiration rates with respect to different environmental drivers.

2. Materials and methods

2.1. Site description and soil sampling

Soil samples were collected from a highland grassland at the NamCo basin in the Tibetan plateau during a field campaign in September 2018. The sampling site was mainly covered by *Kobresia pygmaea* and has been grazed intensively by yaks and sheep. The area is known for its long and

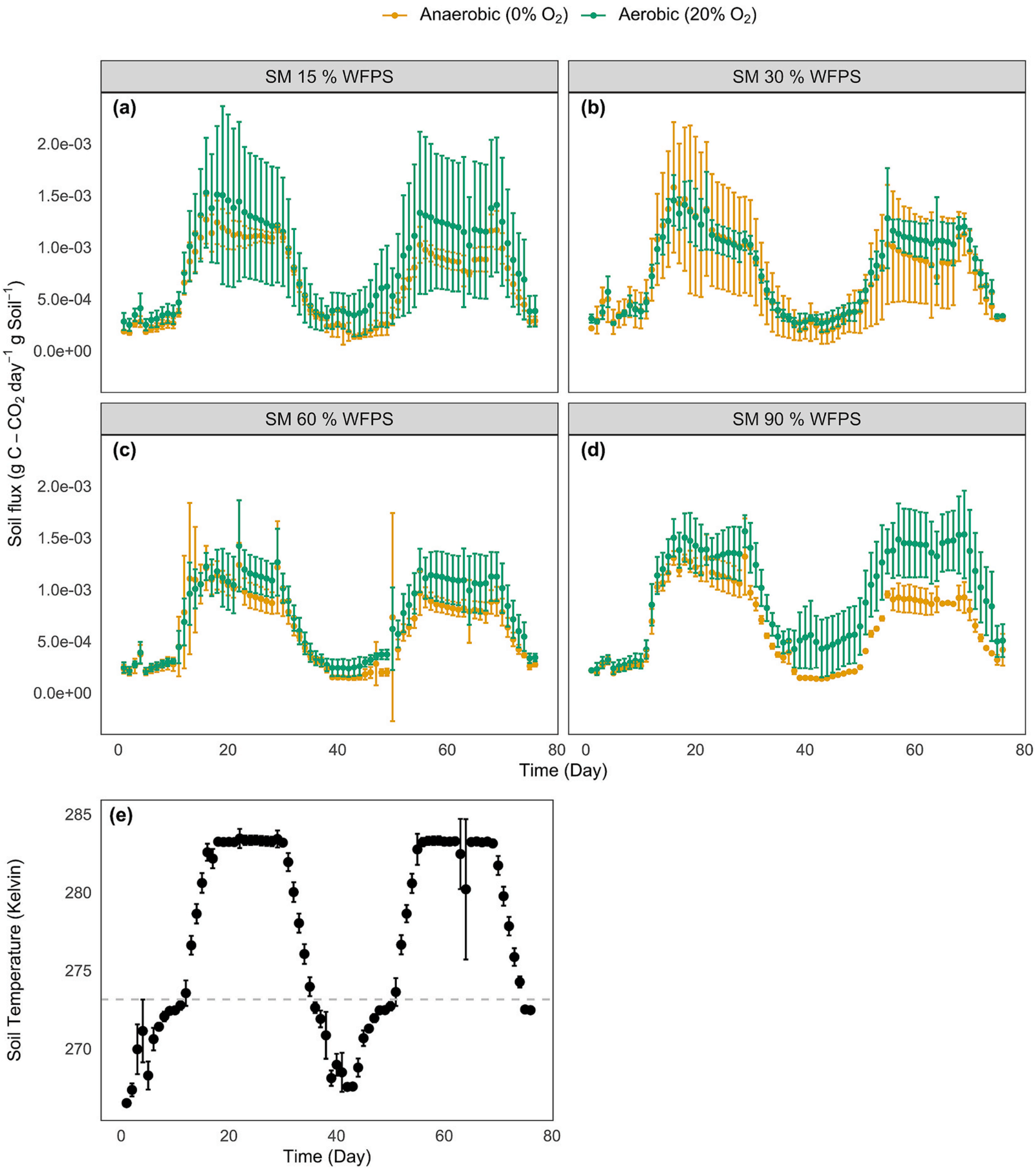

Fig. 2. Amount of C respired in CO_2 during two cycles of freezing and thawing per gram of soil (a–d). Error bars represent the standard deviation among replicates for each treatment. Soil temperature during incubation experiment (e).

freezing winters and short summers. Mean annual temperature is +5 °C and mean annual precipitation is 400 mm (Anslan et al., 2020). For this study, we collected soil samples (5–15 cm depth) using a spade from randomly selected locations from an area of about 40 m^2. A total amount of 40 kg of soil samples were mixed to produce one homogenized sample, and separate portions were placed in airtight plastic bags to keep moisture at field water content prior to preparation for the laboratory experiment. The soils was a sandy loam with an average of 3.63% organic carbon, and a pH of 6.86.

The soil was sieved using $<$ 2 mm mesh and all visible roots and plant debris were removed using a twister. An additional undisturbed sample was collected to measure soil physical and chemical properties such as water content, bulk density, pH, organic matter, carbon, and nitrogen contents.

2.2. Incubation experiment

Soil moisture was adjusted three days prior to the incubation at four different levels: 15, 30, 60, and 90% water-filled pore space (WFPS). After adjusting the soil moisture for each treatment level, they were placed in custom-designed PVC columns (10 cm diameter and 20 cm height) and stored in a +2 °C fridge. Our columns were designed in a way that allow air to pass from the bottom to the top of the column, so the concentration of gases in the soil can be controlled. The weight of the soil in each column was equal to 400 g dry soil (bulk density around 0.6 g cm^{-3}) plus/minus the amount of water added/removed (to/from field moist soil) to adjust the moisture level. Each treatment had four replicates (Fig. 1).

Soil columns were placed in two separate temperature-controlled chambers connected to gas inlets and outlets that allowed us to control gas concentration inside each soil column. Two separate levels of O_2 were continuously flushed through each soil moisture level, one with only N_2 gas with ~0% O_2 and the other with synthetic air with 20% O_2 and 80% N_2. Gas was injected at a flow rate of 30 mL min^{-1} for each column. At the gas outlet, we continuously measured the concentration of CO_2 and CH_4 using a cavity ring-down spectroscopy gas analyzer (Picarro G2301; Picarro, Inc., Santa Clara, USA) via an automated multi-port flow selector valve that selected each outlet for each separate

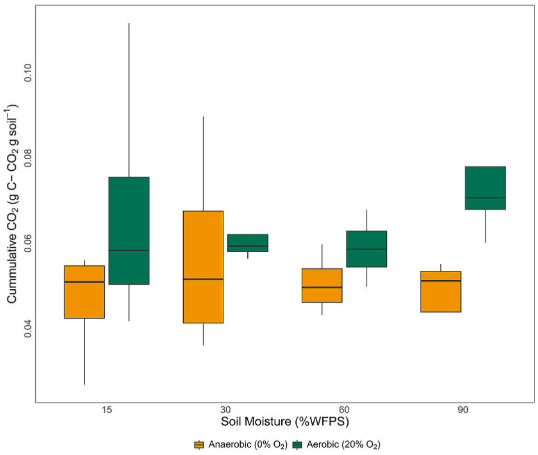

Fig. 3. Cumulative respired CO_2 per each gram of soil over the course of 74 days of incubation with two freeze-thaw cycles and different levels of soil moisture and oxygen. Error bars represent the standard deviation among replicates for each treatment.

column. The concentration of CO_2 and CH_4 in each column was measured twice a day and an average of the two time points was reported as efflux per day. In our incubation experiment, the amount of CH_4 produced was negligible, therefore we only report here CO_2 efflux.

All columns were placed in two chambers with automated temperature adjustment, programmed for the two ramps of freezing-thawing cycles, from −5 to +10 °C. We started the incubation experiment from −5 °C and then the temperature was increased gradually by 2 °C per day until reaching 10 °C. The incubation temperature was held at 10 °C for 14 days and then decreased at a rate of 2 °C per day until reaching −5 °C again. The same temperature program was run in a second freeze-thaw cycle. The soil temperature was continuously measured using thermocouples installed in 6 of the soil columns.

2.3. Data analysis and modeling

We calculated the soil respiration rate $k(t)$ as a function of time t defined as the amount of CO_2 respired per day (Flux $F(t)$ in gC-CO_2 day^{-1}) divided by the initial amount of carbon (C_0 in gC) in each soil column (Eq: 1).

$$k(t) = \frac{F(t)}{C_0}, \tag{1}$$

To evaluate the effect of continuously changing temperature on soil respiration rate for the different levels of soil moisture and oxygen, we fitted the Arrhenius equation to the soil respiration rates separately for each treatment level. The Arrhenius equation has the following form

$$k = A \cdot e^{\frac{-E_a}{\Re T}}, \tag{2}$$

where k (day^{-1}) represents the respiration rate, A (day^{-1}) is the pre-exponential factor and E_a (J mol^{-1}) is the activation energy, $\Re$ (J mol^{-1} K^{-1}) is the Boltzmann constant and T (Kelvin) is the soil temperature. The model was fitted by applying nonlinear least squares approach using the *nls* function in the statistical package R, version 3.6.2 (R Core Team, 2019).

Intrinsic temperature sensitivity was defined as the rate of change of flux rate with respect to the temperature (Lloyd and Taylor, 1994; Sierra, 2012) and expressed as the partial derivative of k with respect to the temperature as:

$$\frac{\partial f(T)}{\partial T} = \frac{\partial k}{\partial T} \tag{3}$$

where $\frac{\partial f(T)}{\partial T}$ is temperature sensitivity (day^{-1} K^{-1}), k is the flux rate

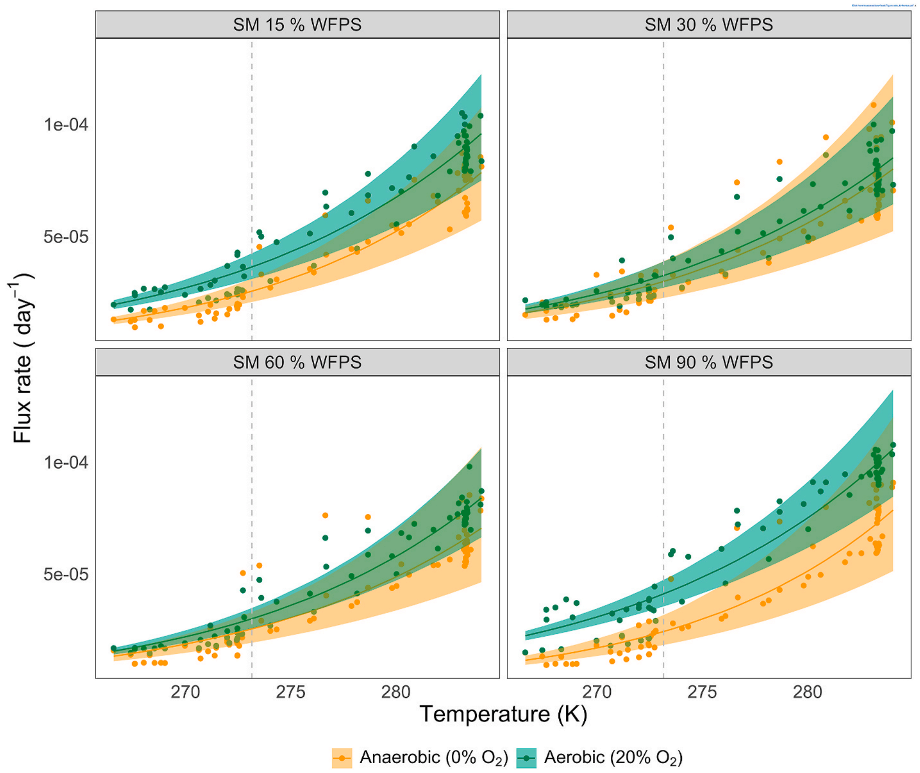

Fig. 4. Soil respiration rate as a function of temperature for different soil moisture and oxygen levels. Curves are the best-fits of non-linear regression (Eq. (2)) to the respiration data for each treatment level. The vertical dashed line corresponds to the freezing point of water, 273 K. Estimated parameter showed in Table 1. The lighted bands around each fitted line represent 5 and 95% model confidence intervals.

Table 1
Summary of fitted non-linear regression model (Eq. (2)) to the respiration data for each treatment level. The highest value estimated for each parameter shown as bold text. All parameter values were obtained with p-values < 0.01. (Units: Soil moisture: % WFPS; Oxygen: %; A: day^{-1}; E_a: J mol^{-1}.)

Soil Moisture	Oxygen	Arrhenius Parameter	Estimate	Std. error
15	0	A	1.5e-05	1.1e-06
		E_a	**6.7e+04**	3.4e+03
	20	A	2.3e-05	1.3e-06
		E_a	5.8e+04	2.6e+03
30	0	A	1.8e-05	1.9e-06
		E_a	5.8e+04	4.6e+03
	20	A	2e-05	1.3e-06
		E_a	5.7e+04	3e+03
60	0	A	1.5e-05	1.6e-06
		E_a	6e+04	4.5e+03
	20	A	1.8e-05	1e-06
		E_a	6.1e+04	2.5e+03
90	0	A	1.4e-05	1.4e-06
		E_a	7e+04	4.6e+03
	20	A	**2.6e-05**	1.4e-06
		E_a	5.6e+04	2.4e+03

Table 2
Summary statistics of obtained posterior parameter values produced by the Bayesian optimization procedure applied to the model of Eq. (6). (Units: k: day^{-1}; E_a: J mol^{-1}; K_M and K_O: in %.).

	k	E_a	K_M	K_O
Mean	4.9e+04	4.7e+04	0.65	0.22
Sd	4.9e+03	2.6e+02	0.05	0.02
Min	3.4e+04	4.7e+04	0.53	0.19
Max	5.3e+04	4.8e+04	0.73	0.24
Median	5.0e+04	4.7e+04	0.65	0.22

calculated by equation (1) and T is the temperature in Kelvin (K). Notice that we use a partial derivative to define intrinsic temperature sensitivity; i.e. the change of the decomposition rate with respect to changes in temperature while other variables are held constant. This definition is useful in our experiment because we kept moisture and oxygen levels constant in the manipulation treatments and only changed temperature.

Equation (3) is a measure of the *absolute* temperature sensitivity, but sometimes it is of interest to compute a metric of the *relative* temperature sensitivity, obtained as

$$\frac{1}{k}\cdot\frac{\partial k}{\partial T}. \tag{4}$$

To asses the consequence of simultaneous changes of three environmental factors on the soil respiration rate we used a simple one-pool carbon model expressed as:

$$\frac{dC(t)}{dt} = -\,\xi(t)\cdot k\cdot C(t), \tag{5}$$

where $\xi(t)$ is a multiplier that modifies the overall decomposition rate k according to changes in temperature, moisture and oxygen. Variable $C(t)$ is the amount of carbon in the system, which changes over time from an initial amount C_0 present at the beginning of the experiment. The function $\xi(t)$ was implemented according to the Dual Arrhenius and Michaelis-Menten (DAMM) model (Davidson et al., 2011), which represents mechanistically the dependance of decomposition rates on three separate functions: one function that captures temperature dependence as an Arrhenius function ($f(T)$), a second function that captures the availability of moisture for the solubility of substrates ($f(M)$), and a third function that captures the availability of oxygen for aerobic decomposition ($f(O)$). Soil moisture and oxygen concentration were considered constant over the course of the experiment.

The form of the time-dependent rate modifier based on the DAMM model can be expressed by the following function:

$$\begin{aligned} \xi(t) \quad &= \quad f(T(t))\cdot f(M)\cdot f(O), \\ &= \quad e^{\frac{-E_a}{\Re T(t)}}\cdot\frac{M}{K_M + M}\cdot\frac{O}{K_O + O}, \end{aligned} \tag{6}$$

where K_M and K_O represent half-saturation constants for soil moisture (M) and oxygen concentration (O), respectively. Notice that the Arrhenius term lacks the pre-exponential factor A present in equation (2) because the decomposition rate k in equation (5) plays the same role. We integrated the DAMM model into equation (5) using the SoilR package (Sierra et al., 2012) and optimized the data produced by the incubation experiment using a Bayesian procedure from the FME R package (Soetaert and Petzoldt, 2010).

The separate intrinsic sensitivities of decomposition rate with respect to temperature, moisture, and oxygen, were obtained using the partial derivative of each function as:

$$\frac{\partial f(T)}{\partial T};\frac{\partial f(M)}{\partial M};\frac{\partial f(O)}{\partial O}. \tag{7}$$

In addition to the model structure defined by equations (5) and (6), we tested other model structures that have biological relevance. First, we tested a model structure that considers explicitly the change in soil moisture as temperature drops below freezing, following a function applied by Tucker (2014) in the context of the DAMM model. We also tested a model structure that considers two carbon pools, one that cycles fast and another that cycles slow, with the idea that only a proportion of the total carbon responds to the experimental treatment within the time frame of this experiment. We performed a model selection analysis of these different model structures, assessing the degree of non-identifiability of the models with respect to the available experimental data. We used a collinearity index that measures the degree of linear association between parameter pairs (Soetaert and Petzoldt, 2010; Sierra et al., 2015), the higher the collinearity the more difficult it is to uniquely identify parameter values from the data. In addition, we used Akaike's Information Criterion (AIC) to quantify the relative loss of information that results by adding additional parameters to the models. The AIC helps to identify the most parsimonious model that can predict reasonably well the experimental data (*Supplementary Material*).

The model selection analysis showed that the model structure defined by equations (5) and (6) was the most appropriate model among all other models. Therefore, from now on we concentrate on the results obtained from this particular model. The full reproducible code with the formal model selection procedure is available in the *Supplementary Material.*

3. Results

3.1. Soil respiration rate during freezing-thawing cycles at different moisture and oxygen levels

Soil respiration rates responded strongly to our temperature manipulation (Figs. 2 and 4). The respiration rates increased with the ramp in temperatures and declined as temperature returned to below freezing levels. The highest amount of carbon was released when soil temperature reached 10 °C during the first cycle followed by a second peak during the second cycle, with the average values across treatments of $1.41 \times 10^{-3} \pm 0.12 \times 10^{-3}$ and $1.20 \times 10^{-3} \pm 0.20 \times 10^{-3}$ gC-CO_2 day^{-1} g Soil^{-1}, respectively (Fig. 2). Holding the temperature constant at 10 °C for 14 days, the respiration rate showed a slow declining trend, possibly due to depletion of labile carbon. The minimum value of flux

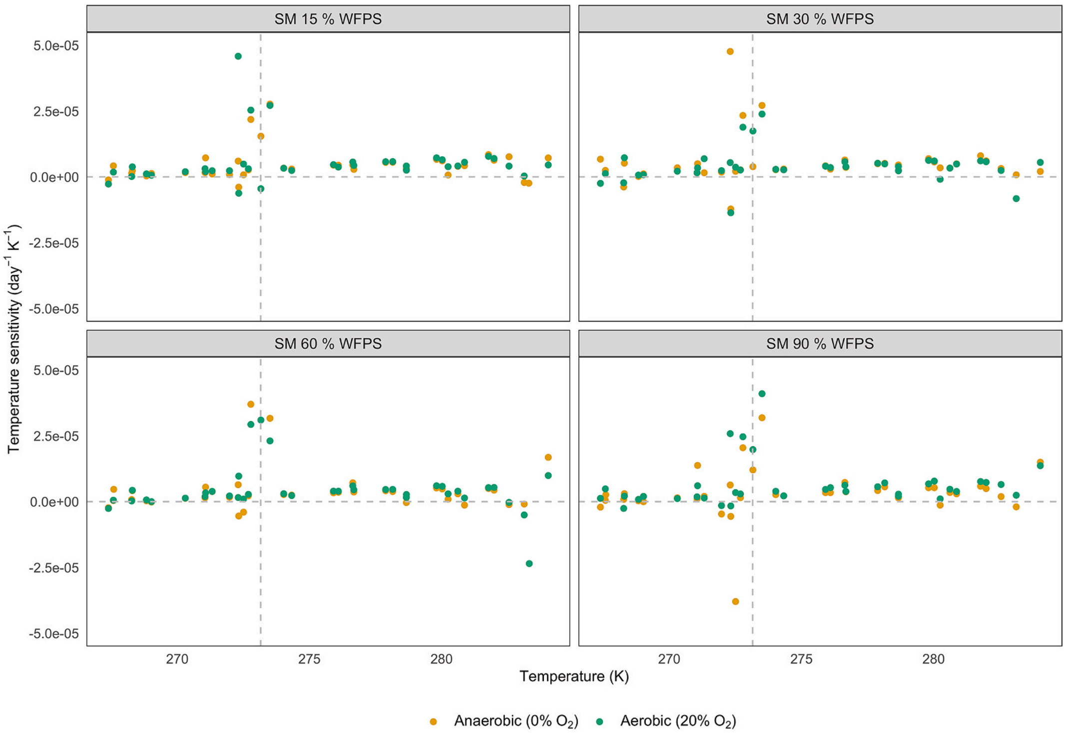

Fig. 5. Soil temperature sensitivity measured as the rate of change in flux rate with respect to change in soil temperature ($\Delta k/\Delta T$).

occurred when soil temperature was at − 5 °C with an average of 1.5 × 10^{-4} ± 0.09 × 10^{-4} and 2.4 × 10^{-4} ± 0.31 × 10^{-4} gC-CO$_2$ day^{-1} g Soil^{-1} for anoxic and aerobic conditions, respectively.

The presence or absence of oxygen had a significant effect on the total amount of CO$_2$ respired during the entire incubation experiment (F statistic p-value < 0.001 from an ANOVA test) (Fig. 3). Although soil moisture alone did not have a significant impact on the quantity of the total cumulative flux (F statistic p-value $= 0.06$), the interaction between soil moisture and oxygen availability did have a significant effect (F statistic p value < 0.001). Overall, the total cumulative flux was higher when oxygen was sufficiently provided, but the saturated soil (90% WFPS), as well as dry soil (15% WFPS), showed a stronger response to oxygen availability than soils of intermediate WFPS . In both cases, aerobic soil respiration was remarkably higher than those in anaerobic conditions. The largest difference between two levels of oxygen was observed when soil moisture was at the nearly saturated conditions (90% WFPS) (Fig. 3).

3.2. Dependence and sensitivity of respiration rates with respect to changes in soil temperature

For each treatment, soil respiration rate showed a strong dependence to temperature and presented good fits to the Arrhenius equation (Eq. (2), Tables 1 and 2). The pre-exponential factor A for the Arrhenius equation was larger for the treatment with 90% moisture and 20% oxygen (Table 1), suggesting that base respiration rates were larger for this particular treatment combination where enough water, oxygen, and temperature were available for aerobic respiration. The activation energy term E_a was larger for the treatment with 15% moisture and 0% oxygen (Table 1).

The sensitivity of respiration rates with respect to temperature for constant levels of oxygen and moisture ($\Delta k/\Delta T$) was nearly the same for the entire temperature range (F statistic p-value $= 0.942$ from an ANOVA test). However, in the vicinity of the freezing point of water, the temperature sensitivity showed a very high level of variability (Fig. 5). Nevertheless, there was no considerable effect of soil moisture and oxygen concentration on the temperature sensitivity of respiration rates.

Although the Arrhenius equation provided a relatively good fit to the observed data, a moderate hysteresis pattern was observed in which the increase in respiration rate was faster for the temperature increase part of the cycle, and slower for the temperature decrease phase. This hysteresis effect can be addressed mathematically by using a dynamic model (equation (5)) that accounts for the changes in available substrate as decomposition proceeds.

3.3. The influence of the simultaneous change of temperature, moisture, and oxygen on decomposition rate

The optimized DAMM model was able to track well the overall trend in the observed flux data (Fig. 6). Model predictions were within the uncertainty range of the observations, however the Bayesian optimization procedure reveled parameter identifiability issues (Fig. S4). We obtained strong correlations between the posterior values of k and E_a, which indicates collinearity and implies that the value of one parameter can be modified proportionally by the other without affecting the overall fit of the model. This is a well-known issue with complex soil carbon models (Luo et al., 2009; Wetterstedt and Ågren, 2011; Sierra et al., 2015; Marschmann et al., 2019), and although our model is relatively simple, parameter values cannot be uniquely identified with the data from our experiment.

Nevertheless, the obtained parameter values provided useful insights on the dependence and sensitivity of decomposition rate with respect to multiple environmental drivers. The results of the model optimization confirmed that temperature is the most important driver for SOC decomposition, while moisture and oxygen limit the decomposition only at the extreme values of their range (Fig. 7). By rising temperature from below freezing levels, decomposition rates increase monotonically across the entire range of temperature (Fig. 7a). Similarly, the intrinsic sensitivity of decomposition rate with respect to temperature follows a monotonically increasing trend (Fig. 7b).

The dependence and sensitivity of decomposition rate with respect to soil moisture and oxygen concentration follow contrastingly different

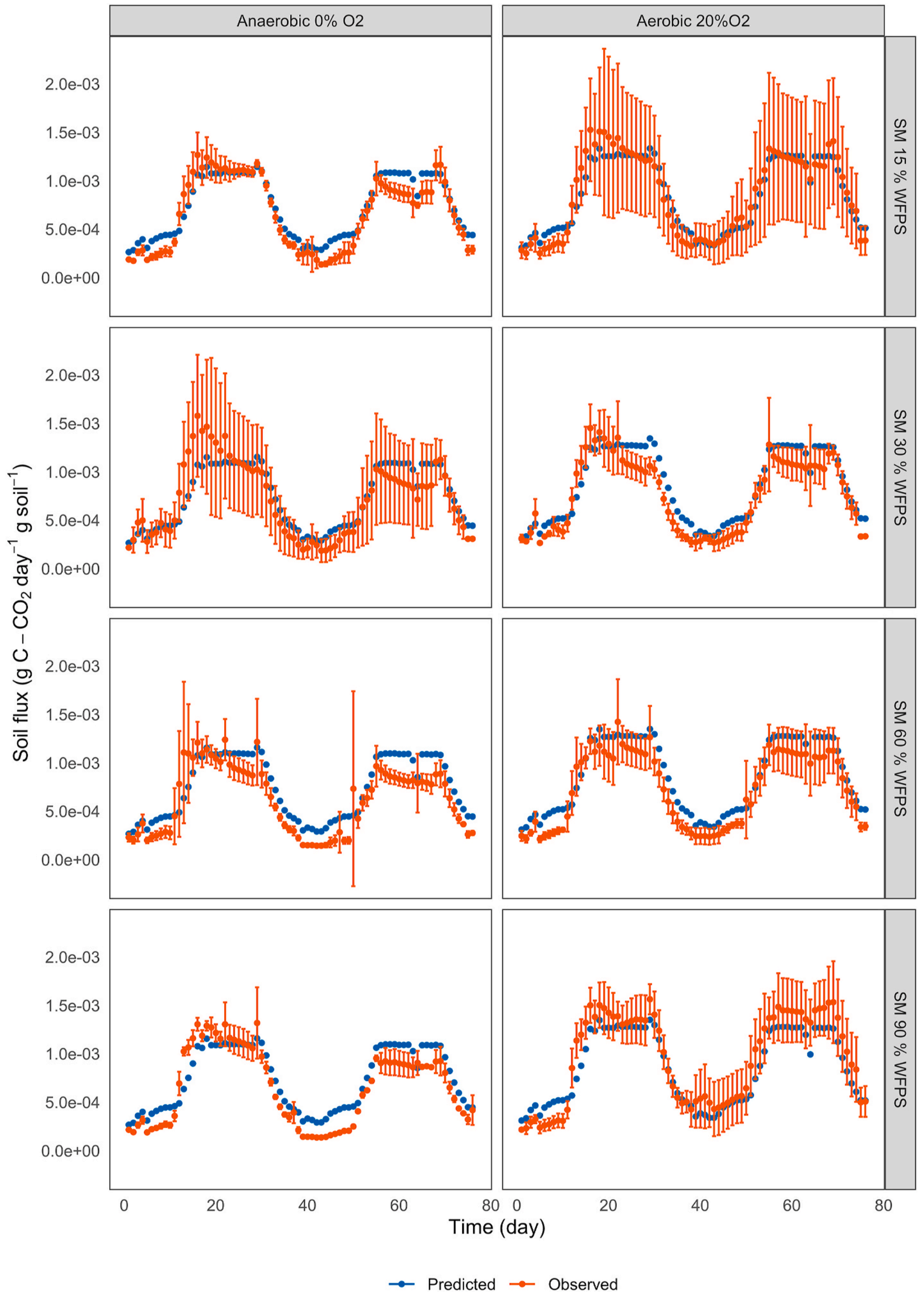

Fig. 6. Observed and predicted flux rates during the experiment for the one-pool model of equations (5) and (6), with parameters obtained though a Bayesian optimization procedure.

patterns in comparison to temperature. Both variables limit rates of decomposition only at their extremes; i.e. under fully dry or fully anoxic conditions (Fig. 7d, f). Once moisture and oxygen became available, even in very small proportions, the decomposition rate is highly sensitive to small changes first, but then it is insensitive to further changes in these variables (Fig. 7d, f).

4. Discussion

4.1. *Response of soil respiration rate to the interaction among soil temperature, moisture and oxygen in freezing-thawing cycles*

The results presented here showed that temperature was the dominant control of respiration rates in all treatment combinations, while interactions with moisture and oxygen were only relevant in treatments with very high or very low moisture availability and anoxic conditions. Outside these extreme cases, interactions seem to be small and the change in temperature dominates the soil respiration response.

In cold environments, microbial activity seems to be highly constrained by energy availability, which is relieved by increases in temperature and dominates over other environmental factors. The activation energy E_a from the Arrhenius equation is a parameter that quantifies this temperature-related energy limitation. Our results showed that E_a differs for different treatment combinations, and that the interaction between moisture availability and oxygen concentration has an effect on the amount of energy required for decomposition to take place. E_a was higher under anoxic conditions in very dry soil, which implies that in the absence of moisture and oxygen, more energy is required for decomposition to proceed (Table 1). The need for more energy in this treatment combination results in lowest rate of respiration

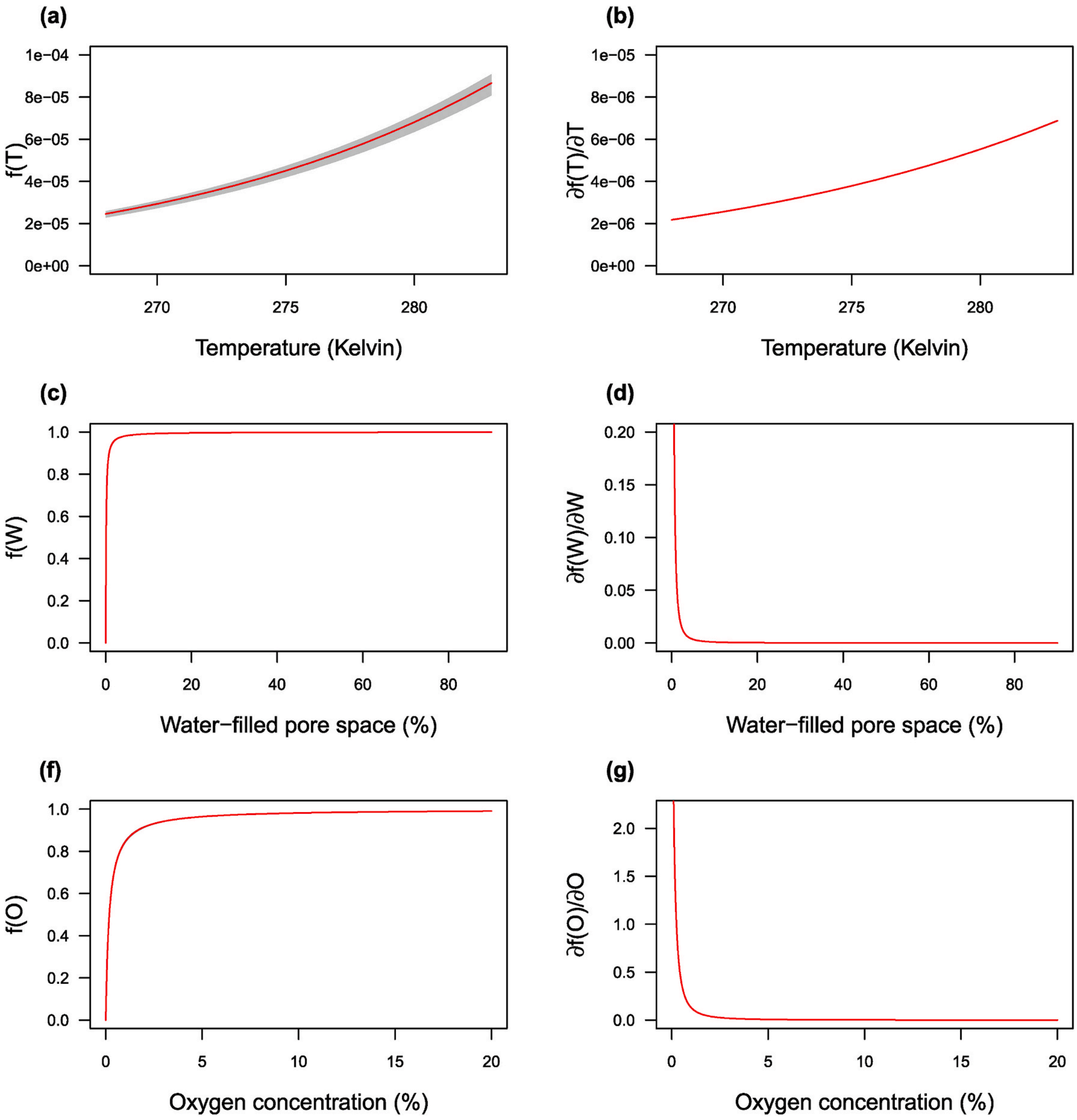

Fig. 7. Soil respiration rate modifiers of the DAMM model with respect to soil temperature, soil moisture and oxygen concentration ($f(T)$, $f(M)$, $f(O)$ in left panels, respectively) and their sensitivities as $\partial f(T)/\partial T$, $\partial f(M)/\partial M$, and $\partial f(O)/\partial O$ in right panels, respectively. Red lines represent the value of each function obtained as the mean of the posterior parameter values obtained from the Bayesian optimization. The gray bands around the red lines represent the value of the functions obtained from the 25 and 75% quantiles of the distribution of the posterior parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

among all treatment combinations (Figs. 2 and 4).

In contrast to our results, other studies performed at temperatures higher than 10 °C have shown a stronger degree of interactions between temperature, moisture, and oxygen availability (Davidson et al., 2011; Sierra et al., 2017; Tucker and Reed, 2016). At higher temperatures, small changes in moisture and oxygen availability may have a stronger effect on decomposition rate than at low temperatures characteristic of high-elevation and high-latitude environments.

Our specific automatic incubation setup allowed us to measure the soil efflux twice a day, providing observations on the relatively fast response of microbes to changes in temperature. This fast response provides strong evidence to the idea that temperature alone was the main driver of the microbial response we observed, expressed as CO_2 efflux.

Two main mechanisms are commonly invoked to explain the fast increase in respiration rates after thawing. First, upon each thawing event, the induced microbial lysis during the freezing phase increases the amount of labile carbon that is newly available to other microorganisms, inducing a priming effect (Skogland et al., 1988; Schimel and Clein, 1996). Second, melted soil water may create a sudden increase in soil moisture, which resembles the Birch effect, the respiration pulse after rewetting due to available water content for microbial activity (Birch, 1964). However, the change in decomposition rate with respect to temperature ($\Delta k/\Delta T$) calculated from the data for all treatments, showed a relatively constant sensitivity across the entire temperature change, except close to the freezing point of water (Fig. 5), which suggests that microbial lysis and the Birch effect may play a role only on a narrow range around 0 °C.

Although our data showed a moderate hysteresis loop, with faster respiration rates with temperature increase and slower rates with temperature decline, this effect can be easily explained in the context of the dynamic model (equation (5)). Our simple one pool model accounts for the fact that less carbon is available for decomposition in the declining phase after temperature was held constant at 10 °C compared to the

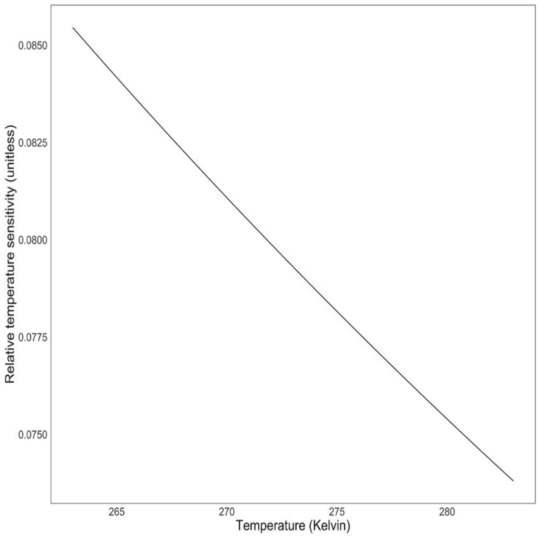

Fig. 8. Intrinsic relative sensitivity ($1/k \cdot \partial k/\partial T$) computed as $E_a/(\Re\ T^2)$ with the average value of activation energy obtained from the Bayesian optimization procedure, $E_a = 47419.95$ J mol^{-1}.

preceding temperature increase. The model can capture relatively well these differences in upward and downward phases of the temperature change, and provides a parsimonious explanation for the observed hysteresis loops.

4.2. Independent and simultaneous change in temperature, moisture and oxygen

One of the main uncertainties in SOC decomposition modeling is in predicting the dependence and the sensitivity of SOC decomposition at low temperatures, especially around the freezing point of water, which occurs predominantly in alpine and arctic areas. Our modeling approach, allowed us to obtain intrinsic sensitivities of decomposition rate with respect to temperature, water content, and oxygen concentrations. These intrinsic sensitivities revealed that temperature (energy) was the main factor that limited decomposition at low temperatures when moisture and oxygen were sufficiently available. Intrinsic sensitivities with respect to soil moisture and oxygen concentration are only relevant at very narrow ranges, when soils are nearly dry or nearly anoxic, and small changes within these narrow ranges may lead to very strong changes in decomposition rate.

Our metric to assess intrinsic temperature sensitivity ($\partial k/\partial T$), showed that it increases as temperatures increase (Fig. 7), although with high variability when obtained from the observed data (Fig. 5). This finding seems to be in contrast with previous studies (e.g. Schmidt et al., 2008; Tilston et al., 2010) that report large temperature sensitivities at low temperatures assessed with the temperature coefficient Q_{10}. However, this perceived contrast is only due to the metric used to assess temperature sensitivity. The coefficient Q_{10} quantifies temperature sensitivity relative to the actual value of the decomposition rate (Sierra, 2012), which is equivalent to computing $1/k \cdot \partial k/\partial T$. Fig. 8 shows that the relative temperature sensitivity of decomposition rates obtained from our model is larger at low than at high temperatures, consistent with previous studies based on Q_{10}s.

Together, our results demonstrate that temperature is the most important factor in controlling changes in decomposition rates in our studied Tibetan grasslands, and further warming climate would have a strong effect on the carbon cycle of the region.

4.3. Opportunities and limitations

The simplified version of the DAMM model we used in this study allowed us to obtain intrinsic sensitivities of decomposition rate with respect to changes in temperature, moisture and oxygen availability under controlled laboratory conditions. Model parameters were derived from the experimental data alone, resulting in a parsimonious model that explains the data well.

However, this model may have important limitations for applications in ecosystem level studies where additional biotic and abiotic controls covary. Nevertheless, we believe there are important opportunities to test our model under field conditions where the main three environmental variables change concurrently. Temperature, moisture and oxygen availability generally show strong co-variability under field conditions, and if field data or a model is available that captures this co-variability, it would be possible to run our model including this information and test against observed data.

In ecosystem level studies, due to the continuous and simultaneous changes in multiple biotic and abiotic factors, the intrinsic temperature sensitivity is not possible to obtain directly from the data, but only with the help of a model (Davidson and Janssens, 2006; Sierra et al., 2015). The full version of the DAMM model can capture most of the dynamic interactions between temperature, moisture and oxygen, but requires site level parameterizations from field observations (Davidson et al., 2011).

5. Conclusion

Controlled laboratory experiments are critical for identifying the main mechanisms governing the greenhouse gas release from soils. Using a full-factorial experimental design coupled with a model optimization approach, we were able to estimate the intrinsic sensitivity of soil respiration rate with respect to changes in soil temperature, soil water content and oxygen availability. Our results showed that temperature in these cold alpine grasslands is the main driver of SOC decomposition rate, and dominates over the effect of moisture and oxygen availabilities. Nevertheless, our results suggest that under anoxic conditions more energy is required for decomposition to proceed.

Despite remaining uncertainties in our model due to parameter identifiability, we can predict that the interaction between temperature, soil moisture and oxygen concentrations in the soil pore space, are only relevant for decomposition at the extremes of very low moisture and very low oxygen levels. Thawing of permafrost in convex landscapes may lead to saturated and anoxic conditions where decomposition rates are limited by oxygen availability. In contrast, areas with steep slopes and exposed to high levels of solar radiation, may also experience strong decreases in decomposition rates due to very dry conditions. Based on our model, we predict that only these areas may have strong sensitivities of decomposition rate with respect to changes in soil moisture and oxygen availability. In other areas in the Tibetan plateau, it is likely that decomposition rates are mostly controlled by temperature changes and are almost insensitive to changes in moisture and oxygen availability.

Declaration of competing interest

Acknowledgements

We would like to thank all colleagues who contributed to this study, especially Dr. Nicole Börner for providing support during field work campaign, and Dr. Karl Kübler for important technical support with the laboratory setup. This study was developed as part of the International Research Training Group (GRK 2309/1) Geo-ecosystems in transition on the Tibetan Plateau (TransTiP) funded by the Deutsche Forschungsgemeinschaft (DFG).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108488.

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CHAPTER 6

Conclusion

This dissertation and the studies included in it have demonstrated that: (1) controlled laboratory experiments are critical for identifying key mechanisms controlling the release of greenhouse gases from soils. However, when implementing complex models in data from incubation studies, the principle of parsimony and the plausibility of the estimated parameters must be verified in advance. (2) Interactions between temperature, soil moisture and oxygen concentration at low soil temperatures are only relevant for decomposition at very low moisture and very low oxygen levels. Beyond these extremes, the decomposition rate depends almost exclusively on soil temperature.

6.1. General conclusion

Despite the considerable progress in understanding terrestrial carbon feedbacks with the atmosphere, there are still large uncertainties in estimating the overall dynamics of carbon in alpine areas such as the Tibetan Plateau. One of the main contributors to this uncertainty is the heterogeneity of the landscape and the high vulnerability to rapid climate change in those areas. The Tibetan Plateau is currently experiencing rapid warming, nearly three times the global average (Qiu, 2008), which impacts a number of biotic and abiotic factors, particularly the overall landscape balance.

Another important source of uncertainty is the divergence between empirical and modeling approaches in predicting the effects of abiotic factors on soil carbon dynamics. A number of available biogeochemical models that analyze the decomposition rate of soil organic carbon have been developed based on functions that indicate the effect of soil temperature and moisture such as Century (Adair et al., 2008) and DayCent (Kelly et al., 2000). However, there is a significant amount of disagreement among these functions for predicting decomposition rates, most notably at different soil moisture levels (Sierra et al., 2015). This dissertation unveiled several sources of the paradox in predicting the effect of abiotic variables on soil organic carbons decomposition rates in the Tibetan Plateau.

6.2. Response of SOC decomposition to the change in environmental factors

Chapter 1 and 2 presented an overview of the major gaps of knowledge in the predicted decomposition rates of soil organic carbon in alpine grasslands of the Tibetan Plateau. The rate of decomposition of soil organic carbon is primarily determined by the interaction of various environmental factors such as temperature, soil moisture, and soil texture. (Sierra et al., 2015). In fact, the interaction between these factors determines whether soil acts either as a sink or a source of carbon. Hence, one of the major sources of this variability is the low predictability of interactions in environmental variables in affecting decomposition rates, which can counteract each other or amplify decomposition as they change simultaneously. This simultaneous change can occur more strongly in the colder temperature mostly due to the consecutive variation in the physical form of soil moisture. In the growing seasons of the cold Plateau, for instance, soils may experience at least one freeze-thaw cycle during a day due to the high fluctuation in soil temperature between days and nights (-5 °C during nights to +25 °C in days) (Nieberding et al., 2021). The freeze-thaw cycles might occur more often during the non-growing season of alpine grasslands of the Tibetan Plateau due to the lower snow coverage during winter time which allows higher solar radiation effects in the daytime.

Below the freezing point of water, soil decomposition rates are constrained by sever shortages in energy (E_a) and substrates (Chapter 5), leading to a strong interplay of three environmental factors that the title of this dissertation emphasis on. In other words, in addition to limitations in energy due to low temperature, soil moisture is highly reduced at these temperatures creating a strong interaction between temperature and low moisture levels. Very low soil CO_2 flux and large reservoirs of accumulated organic carbon in the Tibetan grasslands, can be explained by these limitation in energy and substrate availability, which allowed carbon to accumulate for centuries. Nevertheless, rapid rates in warming, higher solar radiation, and thawed permafrost leads now to the higher source of activation energy and changed this balance rapidly.

Carbon fluxes in alpine steppe biomes are driven by precipitation and temperature, which fluctuate on a daily to seasonal and annual timescale (Nieberding et al., 2021). In chapter 5, my coauthors and I showed that in the relatively cold environments of Tibet, soil temperature is the main driver of soil organic carbon decomposition rate and small increases in soil temperature can increase the decomposition rate of organic carbon. These soils are generally insensitive to soil moisture and oxygen availability, except when soils are so dry or severely anoxic. These findings is in line with other *in situ* measurements that shows how inter-annual flux variability follows the varying monsoonal precipitation. These studies found Tibetan grasslands as a sink of carbon in years with higher levels of precipitation during monsoon seasons while the Tibetan grasslands had a stronger tendency towards functioning as a carbon source in drier years (Wang et al., 2016, 2020, Zhu et al., 2015).

Close to the water freezing point, is the point where microbial activity starts increasing by availability of moisture and oxygen, although it is still restricted by low temperatures (Schimel and Gulledge, 1998). As the grasslands on the TP are widely used for yak and sheep grazing, carbon cycling is influenced particularly through human activities and the degree of soil degradation. Overgrazing in alpine pastures is one of the most frequently mentioned causes of pasture degradation (Harris, 2010, Unteregelsbacher et al., 2011), as excessive trampling by livestock might aggravate the initial conditions of polygonal cracking (Miehe et al., 2019). Degraded grasslands are even more sensitive to changes in temperature (Pei et al., 2022), and small increases in temperature will further increase the losses of soil organic carbon, making the ecosystem more vulnerable to climate change.

Additionally, the region is a heterogeneous area not only in terms of landscape and vegetation cover but also in soil water level, comprising alpine meadows, alpine steppes, wetlands, and highlands (JingYun et al., 2010). In such a complex ecosystem, together with inaccessibility to such a remote region which introduce restrictions for direct monitoring of microbial decomposition rates, integrating laboratory incubation measurement with mathematical models serves as an important approach for investigating the key parameters governing the decomposition process (Schädel et al., 2020). Yet, there are limits to the levels of complexity that mathematical functions can be used to explain patterns in the laboratory experiments, and parsimony models are often preferred over complex models.

6.3. Parameterization of SOC models from incubation data

In chapter 3, I emphasize the importance of model selection techniques by employing different criteria in assessing model performance. I used information theory metrics and the concept of mean transit time to select models that can better predict the experimental data without making additional assumptions on model structure. The knowledge on the timescale that carbon resides in soil, and tracing that in both carbon stock and respired carbon can be used as an indicator to perform fractionation when modeling SOC dynamics. This knowledge at the same time can be used as a criterion to test the uncertainty in model performance, even though the model has been selected as the best model in a model selection analysis. For example, this analysis suggested that regardless of the goodness-of-fit of a model, it is still possible that a model fails in predicting a valid estimate for soil respiration rate after testing them for the calculation of mean transit time.

Furthermore, in chapter 3 I highlighted the importance of the experimental design in providing reliable data to be integrated into the model in order to evaluate details about various soil organic carbon fractions, in addition to decomposition rates of each of the carbon fractions, and transfers among them. In particular, in periodic data acquisition from laboratory incubations, frequent monitoring at the beginning of the experiment is essential, since respiration of fast-cycling carbon dominates total carbon respired, but it declines rapidly (within days). Measurements of a fast-cycling fraction are more precise in short-interval measurements (Chapter3). One of the advantages of the incubation setup in my experimental study was the ability to acquire data frequently during the experiment. I was able to obtain two observation values per day for each treatment/replication levels and report the average of these two observation points as the daily CO_2 respiration rate (Chapter 5), providing observations on the relatively fast response of microbes to changes in temperature. This fast response highlighted the fact that temperature alone was the main driver of the microbial response we observed, expressed as CO_2 efflux.

The use of a two-pool model can provide valuable information on the size of the carbon pool in the soil and its transit time, but estimating the dependence of this carbon pool on abiotic factors requires additional parameters. The addition of parameters has the potential to increase the risk of non-identifiability of model parameters due to high correlation between two sets of parameters. Formal model selection techniques in this case indicated that a single pool-model may be sufficient to capture information from the data in the short course of the study and in predicting temperature, moisture, and oxygen dependencies.

This dissertation also provided valuable insight into the application of modifications in mathematical functions along temperature and moisture gradients with respect to the objective of the study, rather than using other available biogeochemical models. However, any mathematical structure must be controlled for collinearity among estimated parameters, goodness of fit, and validity of the estimated parameters, and the model must also comply with the principle of parsimony.

Our findings emphasize the implication of different criteria in model selection performance. The knowledge on the timescale that carbon resides in soil, and tracing that in both carbon stock and respired carbon can be used as an indicator to perform fractionation when modeling soil organic carbon dynamics. This knowledge at the same time can be used as a criterion to test the uncertainty in model performance, even though the model has been selected as the best model in a model selection analysis. Therefore, we see a great potential for using radiocarbon information in incubation experiments to assist in the model selection process. Radiocarbon provides extra information on the time that carbon atoms have remained in the soil or in the soil respiration flux. The mean transit time of carbon predicted from a model, can therefore be compared with the radiocarbon values of respired CO_2 from an incubation and be used as an additional constraint to select the best model.

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APPENDIX A

Supplementary information: Sensitivity of soil respiration rate with respect to temperature, moisture and oxygen under freezing and thawing

Supplementary material of

Sensitivity of Soil Respiration Rate with Respect to Temperature, Moisture and Oxygen under Freezing and Thawing

Azizi-Rad M. et al.

Abstract

This document presents a model selection analysis to identify the most appropriate model structure to represent the data from the incubation experiment presented in the manuscript. Five different model structures were assessed: Model 0 is the simplest model structure, fitting only the DAMM rate modifiers to the data. Model 1 includes a base decomposition rate that is modified by the DAMM rate modifiers. Model 2 adds a function that relates temperature and moisture below the freezing point of water. This structure helps to represent the effects of freezing in reducing water availability for decomposition. Model 3 uses two carbon pools instead of one, with the idea that only one fraction of the total carbon responds to the experimental treatments. Finally, Model 4 includes both a function relating temperature and moisture below the freezing point of water, and two separate carbon pools. These five model structures were evaluated using a collinearity index that measures the strength of linear relation among parameter pairs and indicates non-identifiability problems. We also used the Akaike's Information Criterion AIC to find the most parsimonious model that can best predict the data. We found important non-identifiability problems in models 1, 2, and 4, which indicate that the experimental data does not provide enough information to uniquely identify all model parameters for these model structures. According to the AIC, the most parsimonious model that better predicts the data was Model 0; however, Model 1 provides better fit to the data and it is easier to interpret in the context of the experimental study. We conclude that Model 1 is the best choice to analyze the experimental results presented in our manuscript.

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Introduction

This document presents a model selection analysis of 5 different modifications of the original Dual Arrhenius-Michaelis Menten Model (DAMM) (Davidson et al. 2011) which can be fitted to the data from our incubation experiment. Here we aim to find the most appropriate model that can represent the incubation experiment data and that is useful to answer the proposed research questions presented in the manuscript.

We considered five different model structures. The most complex model (Model 4) contains two carbon pools, one that reacts fast within the timeframe of the experiment, and another that reacts slow. This model structure also considers a function that relates temperature and moisture below the freezing point of water, with the idea of representing the indirect effect of freezing in reducing soil water content. Model 3 has two carbon pools, but does not contain the relationship between temperature and moisture below freezing. Model 2 contains only one carbon pool, but considers the relation between temperature and moisture below freezing. Model 1 contains only one carbon pool and does not consider the interaction between temperature and moisture. A reduced model was also considered, Model 0, which does not have a base decomposition rate and only fits the parameters of the DAMM model. Details about each model structure are presented below.

For each model structure we evaluated a collinearity index that quantifies the degree of linear relation among two parameters. This index is a measure of the non-identifiability of parameters given the available data. Values of the index above 20 indicate that it is not possible to uniquely identify parameters from the available data. We used the *R Package FME* (Soetaert and Petzoldt 2010) to compute this collinearity index. We also used Akaike's Information Criterion (AIC) to compare the goodness of fit of models considering the number of parameters to identify. Lower values of AIC indicate that a model structure is parsimonious in predicted the available data with the least number of parameters. To assess the goodness of fit alone without considering the number of parameters to fit, we compared the root mean squared error (RMSE).

All models were fit using a Bayesian optimization procedure that uses Markov chain Monte Carlo (MCMC) using as a cost function the squared difference between predictions and all observations from the incubation experiment. Uniform priors were used for all model parameters, and a total of 100,000 chains were ran with 2,000 burn in chains. We used the FME package for these computations (Soetaert and Petzoldt 2010).

Model 0: One-pool model with fixed decomposition rate

We start the model selection analysis testing a one-pool model assuming that the base decomposition rate is constant and equals to one ($k = 1$), and the rate of change of carbon is only influenced by the time-dependent rate modifier $\xi(t)$ (Eq: 1). The differential equation representing the model is given by

$$\frac{dC(t)}{dt} = -\ \xi(t) \cdot k \cdot C(t) \tag{1}$$

where the amount of carbon remainig in the soil after some time t is $C(t)$. The initial amount of carbon at the begining of the experiment is therefore $C(0) = C_0$. The rate modifier $\xi(t)$ was implemented according to the Dual Arrhenius and Michaelis-Menten (DAMM) model as:

$$\begin{aligned} \xi(t) &= f(T(t)) \cdot f(M) \cdot f(O), \\ &= e^{\frac{-E_a}{\Re T(t)}} \cdot \frac{M}{K_M + M} \cdot \frac{O}{K_O + O} \end{aligned} \tag{2}$$

This rate modifier is composed of separate functions that depend on temperature T, the amount of moisture in the soil M and the concentration of oxygen in the soil O. In our experiment, M and O were kept constant, and temperature was changed over time, therefore we express this time-dependency as $T(t)$. The functions that depend on M and O are expressed as Michaelis-Menten functions, therefore they include half-saturation constants K_M and K_O, respectively.

Using this version of the model, we optimized the parameter set: activation energy (E_a), half-saturation constant for soil moisture (K_M), and half-saturation constant for oxygen concentration (K_O).

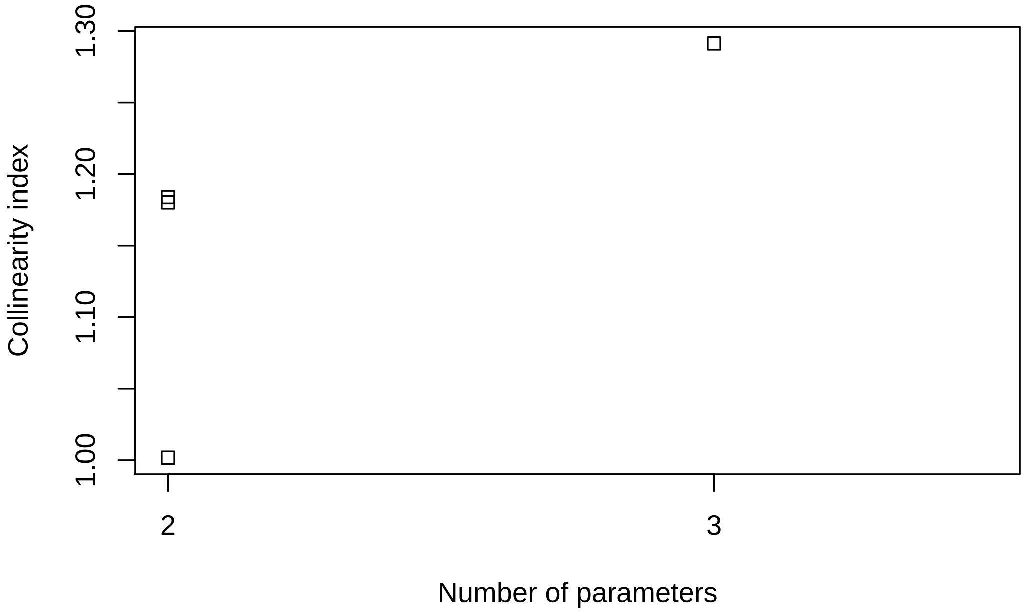

Figure 1: Collinearity index obtained for all possible combinations of parameters in Model 0. All values are below 20, which indicates that this model structure can be uniquely identified with the existing data.

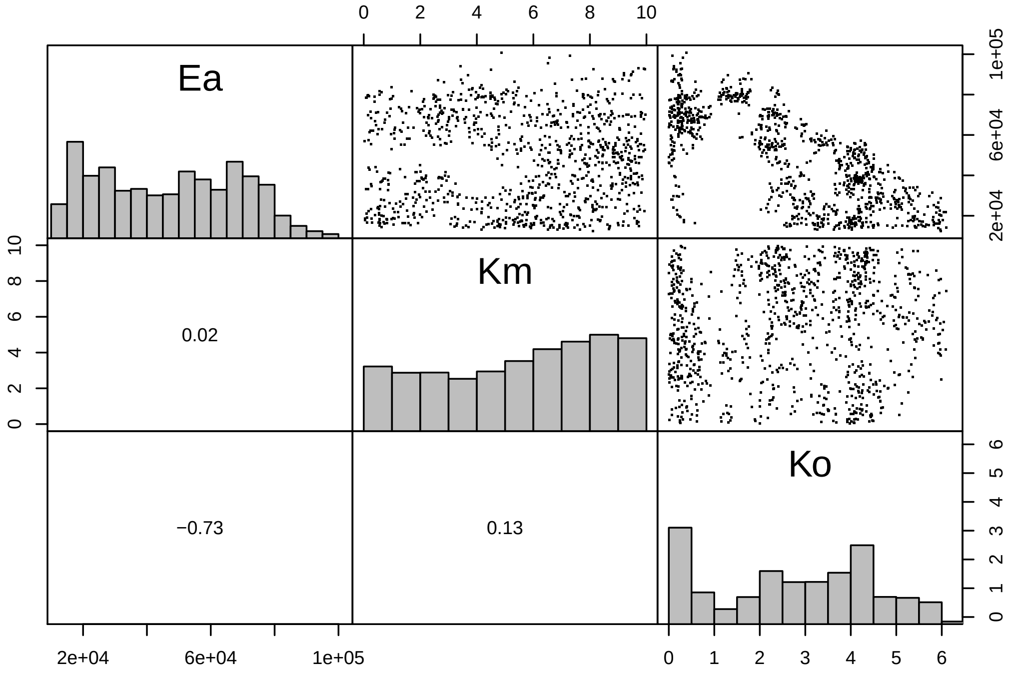

Figure 2: Posterior parameter values from the Bayesian optimization using the full model Model 0. We plot here a subsample of 1000 parameter sets from a total of 100,000.

Table 1: Summary statistics of posterior parameter values obtained from the Bayesian optimization. (Units: E_a: J mol^{-1}; K_M and K_O: in %)

	E_a	K_M	K_O
mean	47180.26	5.538	2.750
sd	22111.50	2.924	1.747
min	12392.70	0.002	0.000
max	100853.72	9.992	6.208
q025	26426.93	2.991	1.056
q050	47760.48	5.976	2.918
q075	66954.65	8.092	4.181

The collinearity index shows that there are no identifiability problems among parameter pairs in this model structure (Figure 1). There are also no signs of strong correlations among posterior parameter values (Figure 2). The obtained RMSE obtained by fitting this model was 0.01 g C-CO$_2$ g Soil^{-1}. The AIC obtained from this model structure was 19.32.

Model 1: One-pool model with unknown decomposition rate

Here we considered the case in which the base decomposition rate k is an unknown parameter that needs to be determined by the optimization procedure. This model structure has been used to analyze the experimental data presented in our manuscript.

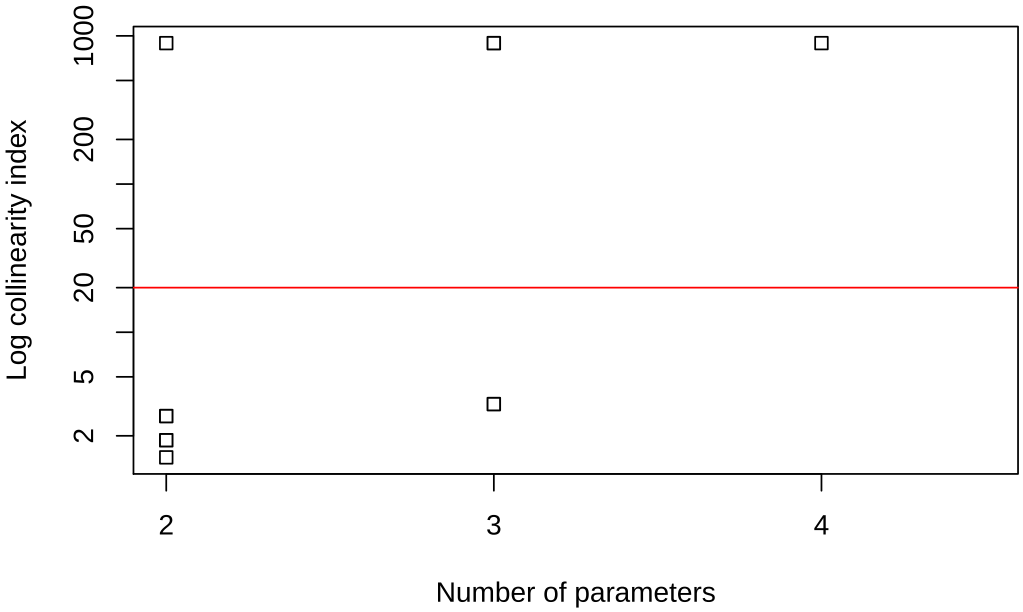

Figure 3: Collinearity index obtained for all possible combinations of in Model 1. The values higher than 20 represent the strong linearity between parameter combinations. A base-10 log scale is used for the Y axis, which ranges from 0.1 to 1,000.

Table 2: Summary statistics of obtained posterior parameter value using a Bayesian optimization. (Units: k:day^{-1}; Ea: J mol^{-1}; K_M and K_O: %)

	k	E_a	K_M	K_O
mean	554507.6	53085.265	0.216	0.177
sd	110916.9	469.559	0.153	0.011
min	347975.6	52046.827	0.001	0.146
max	838866.2	54096.450	1.072	0.216
q025	471759.7	52748.090	0.092	0.169
q050	538808.8	53074.743	0.190	0.176
q075	633608.9	53436.747	0.310	0.184

The values of the collinearity index for 3 parameter combinations including k and E_a are higher than 20, which means that the current available data is insufficient to uniquely identify all model parameters for these model structure (Figure 3). This problem appeared also as a strong correlation between obtained posterior k and E_a values. (Figure 4). The AIC score obtained for this model structure was 63.42. The goodness of fit measured as RMSE was 3.89e-08 g C-CO_2 g Soil^{-1}.

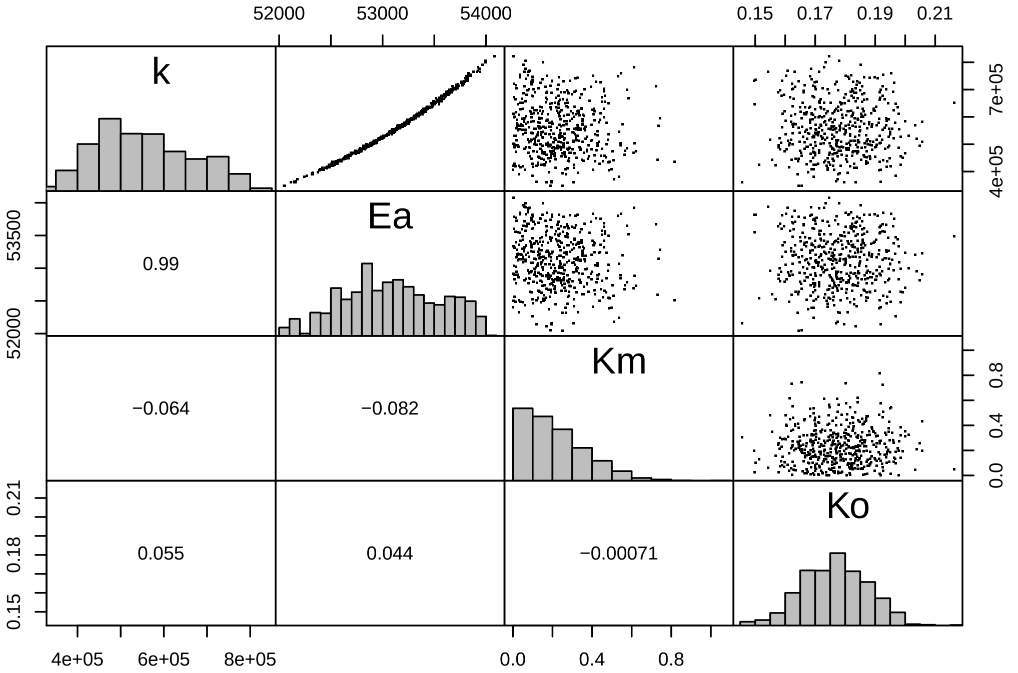

Figure 4: Posterior parameter values from the Bayesian optimization using Model 1. We plot here a subsample of 1000 parameter sets from a total of 100,000.

Model 2: One-pool model with moisture reduction below freezing

This model structure adds a modification to the DAMM model that accounts for the reduction in soil moisture due to the freezing. Based on the Tucker (2014) we assumed the proportion of water availability as a function of temperature and divided the soil moisture in two different phases as:

$$M_{liq} = \begin{cases} M & \text{if} \quad T \geq 0°\text{C}, \\ M \cdot A_m \cdot |T|^{B_m} & \text{if} \quad T < 0°\text{C}, \end{cases} \tag{3}$$

where M_{liq} is the amount of liquid water available for decomposition, which is reduced from a constant value M for temperatures below zero degrees Celcius. A_m and B_m are unknown parameters that vary for different soil types. Due to the lack of available measurements of moisture during the course of the experiment, we added the two parameters of A_m and B_m to the set of parameters to identify in Model 2.

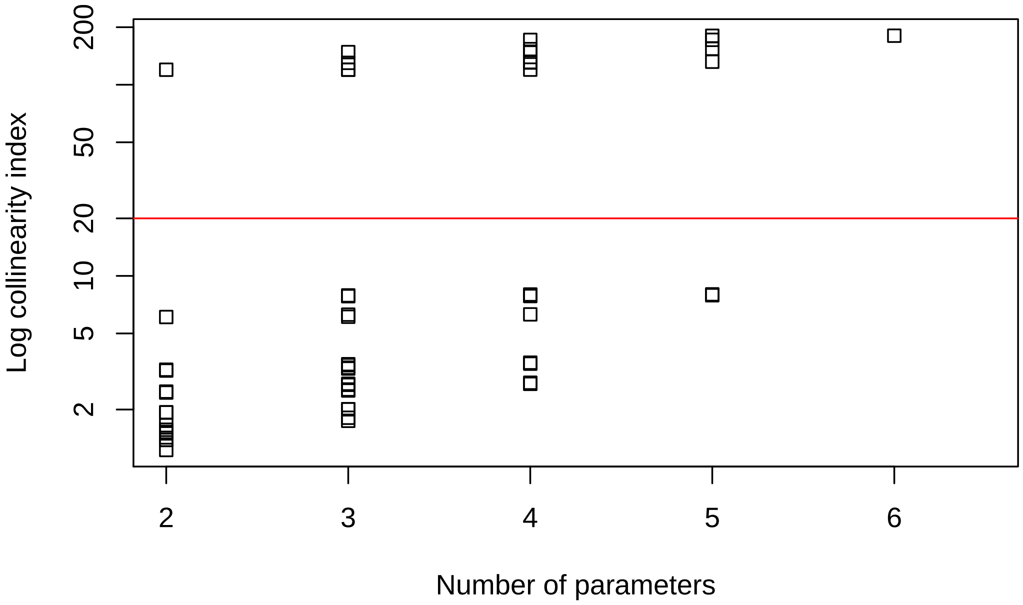

Figure 5: Collinearity index obtained for all possible combinations of parameters to identify in Model 2. The values higher than 20 represent the strong linear relation between parameter combinations. A base-10 log-scale is used for the Y axis, which ranges from 0.1 to 1,000.

Table 3: Summary statistics of obtained posterior parameter value using a Bayesian optimization. (Units: k: day^{-1}; E_a: J mol^{-1}; K_M and K_O: %)

	k	E_a	K_M	A_m	B_m	K_O
mean	2138.115	39545.311	0.291	0.016	-0.043	0.172
sd	1434.171	1606.859	0.087	0.006	0.013	0.012
min	610.846	37183.009	0.154	0.010	-0.074	0.137
max	5153.627	42152.690	0.626	0.039	0.000	0.204
q025	853.017	37946.270	0.225	0.012	-0.052	0.164
q050	1480.175	39234.876	0.267	0.015	-0.046	0.168
q075	3582.816	41271.319	0.329	0.020	-0.038	0.180

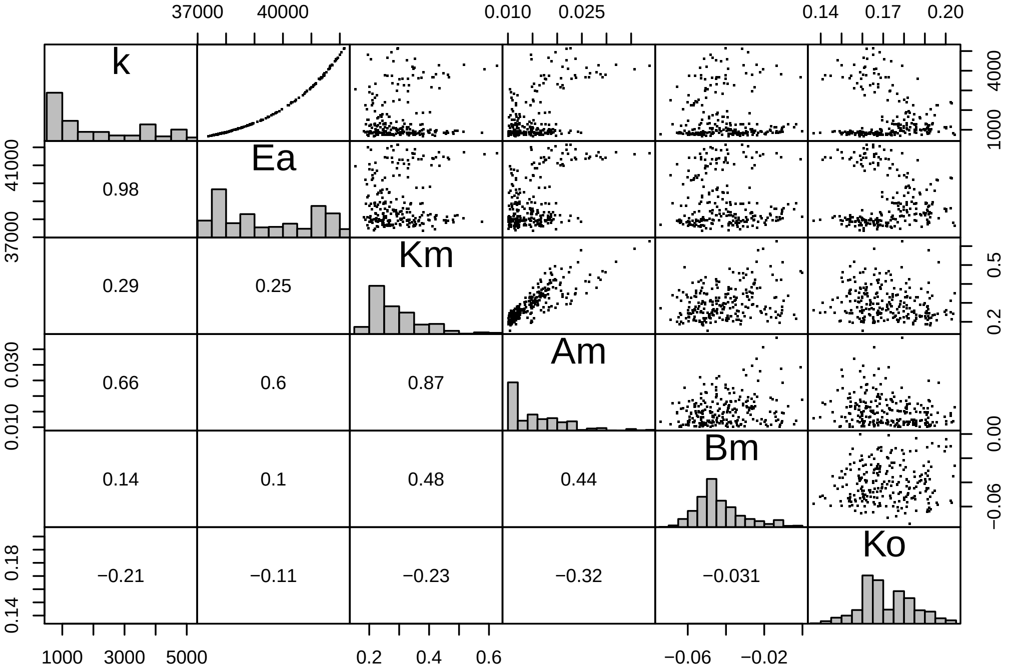

Figure 6: Posterior parameter values from the Bayesian optimization obtained by Model 2. We plot here a subsample of 1000 parameter sets from a total of 100,000.

The collinearity index for parameter combinations including the pair k and E_a were always higher than 20, similarly as in Model 1 (Figure 5). There was a strong correlation between the obtained posterior values of k and E_a as well as K_M and A_m. (Figure 6). The AIC score obtained for this model structure was 67.58. The goodness of fit measured as RMSE was 3.8e-08 g C-CO$_2$ g Soil^{-1}.

Model 3: Two-pool model with constant moisture

Here we assume that there are two pools of carbon, one that decomposes slowly C_2 and one that decomposes fast C_1 and reacts within the timeframe of the experiment. Therefore, we need to assume that the initial amount of carbon in the soil is split by a fixed proportion p, a new parameter that we need to estimate from the available data. The corresponding decomposition rates for each pool k_1 and k_2 (day^{-1}) are modified by the DAMM rate modifier $\xi(t)$, without including a relation between temperature and moisture below freezing. The set of differential equations is given by:

$$\begin{pmatrix} \frac{dC_1(t)}{dt} \\ \frac{dC_2(t)}{dt} \end{pmatrix} = -\ \xi(t) \cdot \begin{pmatrix} k_1 & 0 \\ 0 & k_2 \end{pmatrix} \cdot \begin{pmatrix} C1 \\ C2 \end{pmatrix} \tag{4}$$

The initial amount of carbon in the system C_0 is partitioned according to a proportion p as:

$$C_0 = C_0 \cdot \begin{pmatrix} p \\ 1-p \end{pmatrix} \tag{5}$$

The environmental term ξ is similar to the Model 0 and 1; however, three new parameters: k_1, k_2 and p are now added to the optimization.

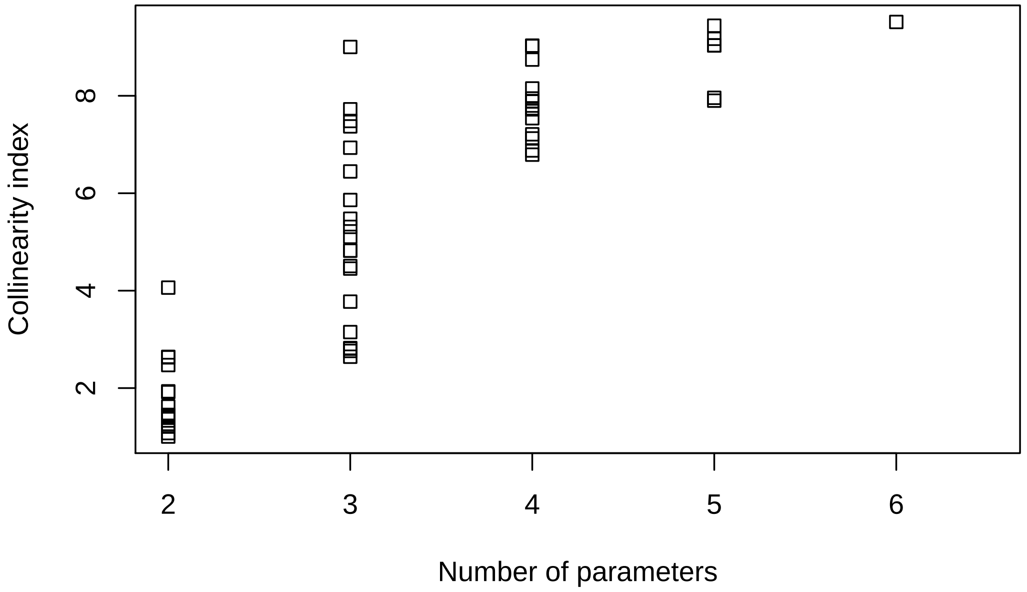

Figure 7: Collinearity index obtained for all possible combinations of parameters from Model 3. All values are below 20, which indicates low linear correlation among parameter pairs.

Table 4: Summary statistics of obtained posterior parameter value using a baysian optimization. (Units: k_1 and k_2: day^{-1}; p: unitless; E_a: J mol^{-1}; K_M and K_O: %)

	k_1	k_2	p	E_a	K_M	K_O
mean	112712.08	9801.772	0.098	43465.819	0.190	0.184
sd	54957.24	202.108	0.039	107.637	0.135	0.009

9

	k_1	k_2	p	E_a	K_M	K_O
min	46628.10	8679.622	0.040	43111.049	0.000	0.157
max	236647.43	9999.965	0.178	43641.116	0.711	0.204
q025	65218.69	9682.988	0.057	43381.332	0.066	0.178
q050	97511.23	9855.461	0.095	43503.468	0.171	0.185
q075	170429.37	9947.623	0.132	43547.160	0.280	0.189

In this model structure the collinearity index showed low values for all parameter pairs (Figure 7), which could be interpreted as if the parameters can be identified from the data. However, the posterior parameter values showed strong nonlinear relations between some parameter pairs, particularly k and p, as well as E_a and p (Figure 8). The colinearity index in this case was unable to show these strong associations between parameter values, but the non-identifiability problem still remains. Changes in one parameter can be compensated by changes in another parameter, and they are strongly related through a particular function. The goodness of fit measured as RMSE was 4.38e-08 g C-CO_2 g Soil^{-1}, and the AIC score obtained for this model structure was 65.59.

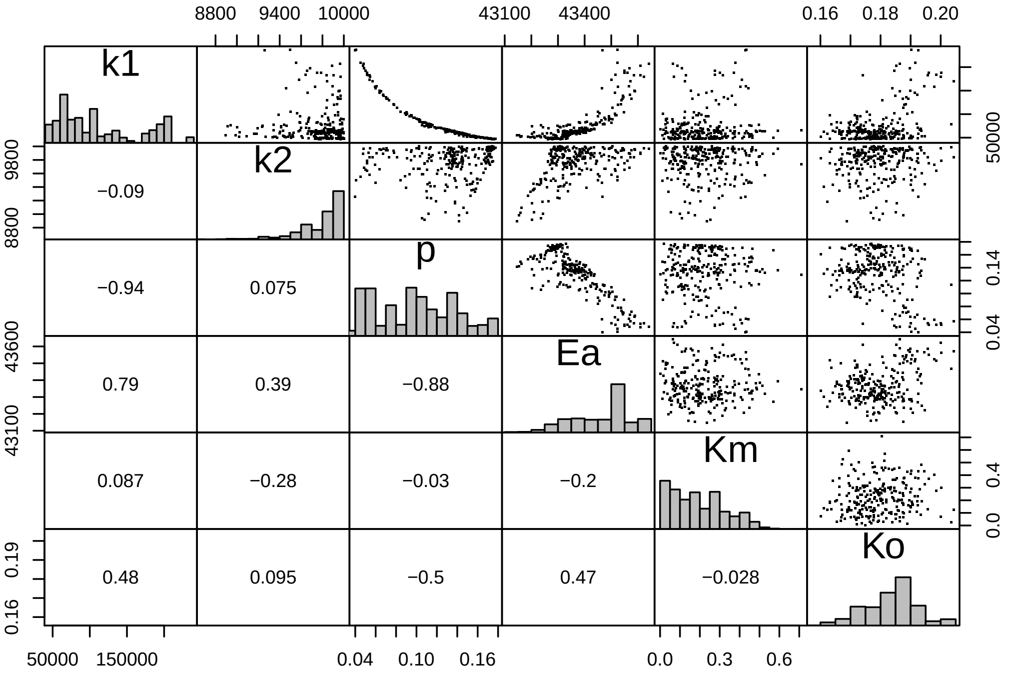

Figure 8: Posterior parameter values from the Bayesian optimization using the full model Model 3. We plot here a subsample of 1000 parameter sets from a total of 100,000.

Model 4: Two-pool model with moisture reduction below freezing

In this model structure, we used the two-pool model structure (Eq. 4) and added a function that relates soil temperature and soil moisture below the freezing point of water (Eq. 3). This is the most complex model among all the models we tested, and considers the optimization of 8 parameters.

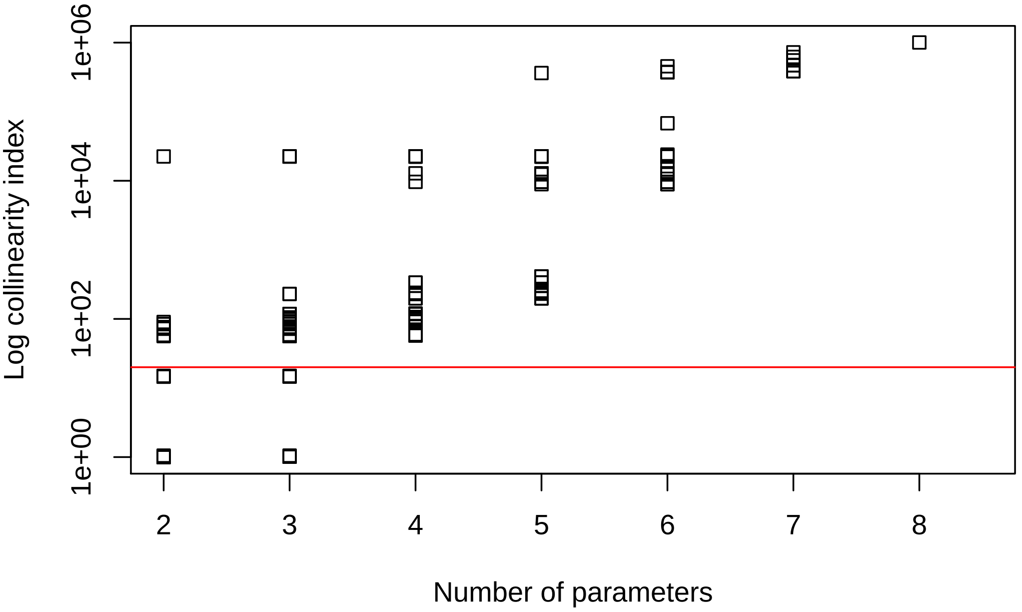

Figure 9: Collinearity index obtained for all possible combinations of Model 4. Values higher than 20 indicate strong linearity between parameter combinations. A base-10 log-scale is used for the Y axis, which ranges from 0.1 to 1,000.

Table 5: Summary statistics of obtained posterior parameter value using a baysian optimization. (Units: k_1 and k_2: day^{-1}; p: unitless; Ea: $Jmol^{-1}$; K_M and K_O: %)

	k_1	k_2	p	Ea	K_M	A_m	B_m	K_O
mean	190209.37	8196.122	0.049	43096.332	0.303	0.178	0.019	-0.042
sd	78518.37	927.512	0.017	270.866	0.105	0.007	0.007	0.010
min	90050.95	6286.654	0.027	42512.221	0.146	0.155	0.010	-0.070
max	344132.46	9998.869	0.095	43597.843	0.538	0.198	0.035	-0.010
q025	133433.17	7509.028	0.036	42904.953	0.210	0.173	0.013	-0.049
q050	168075.59	8173.704	0.046	43091.501	0.283	0.179	0.018	-0.041
q075	240886.85	9051.785	0.060	43309.400	0.381	0.183	0.025	-0.035

The values of the collinearity index obtained with in this model, together with the strong negative and positive correlations between several posterior parameter pairs, indicate that the experimental data does not provide enough information to uniquely identify most of the model parameters for Model 4 (Figures 9 and 10). The obtained squared error of the residuals obtained by fitting this model was 3.57e-08 g C-CO_2 g Soil^{-1}. The AIC obtained from this model structure was 70.41.

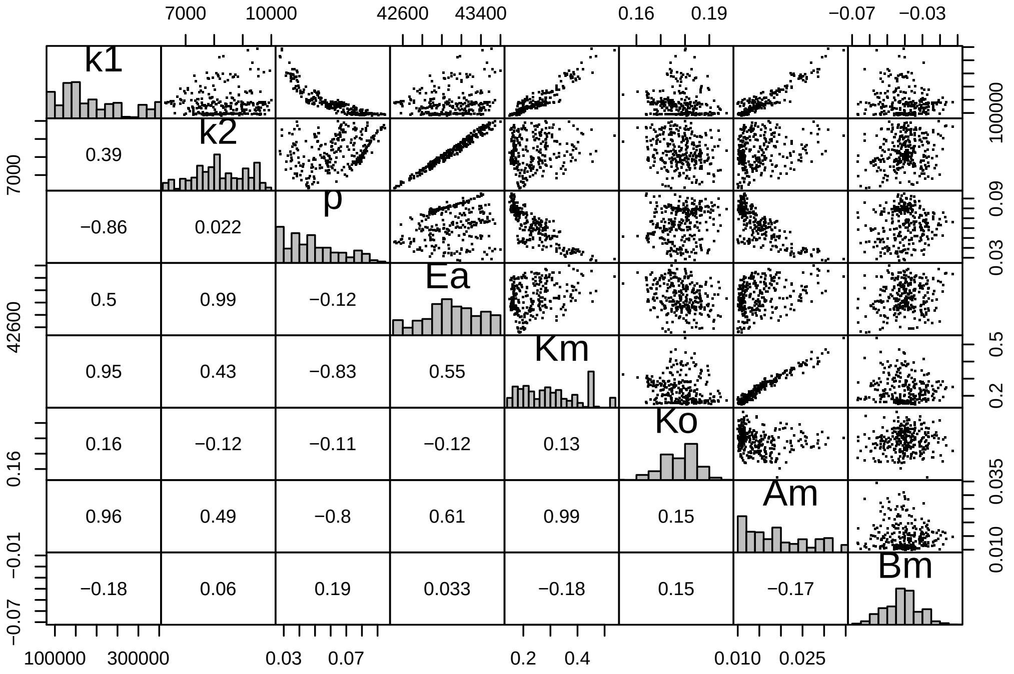

Figure 10: Posterior parameter values obtained from the Bayesian optimization using Model 4. We plot here a subsample of 1000 parameter sets from a total of 100,000.

Conclusions

We evaluated five model structures and used two metrics to assess the degree of non-identifiability of the models, a collinearity index and the correlation among posterior parameter values after Bayesian optimization. We also used the AIC and the RMSE to assess goodness of fit. Based on this analysis we can conclude:

1. All model structures, except Model 0, present identifiability problems. The collinearity index was high for Models 1, 2, and 4; and the correlations among many posterior pairs were strong for all models except Model 0 (Table: 6).
2. According to the AIC, the most parsimonious model is Model 0 because it contains the least number of parameters to identify from the available data. However, Model 0 has a higher RMSE and tends to underestimate the data compared to Model 1 (Table: 6).

We conclude that Model 1 provides the best compromise between model complexity, goodness of fit, and model interpretability. It can predict well the observed experimental data, it gives a value for a base decomposition rate that is affected by the DAMM modifiers, and does not include additional complexity that cannot be supported by the available data. This model still has identifiability problems, which could be improved if additional data were available, e.g. on the quality of the organic material. To identify Models 2, 3, and 4, additional data would be required on changes in soil moisture over time and the size of the different carbon fractions.

Table 6: Comparison of goodness of fit between different version of dynamic models based on the incubation experiment data. Degrees of freedom on the residual standard errors are shown within parenthesis.

Model	Parameter sets	AIC	RMSE
Model 0	E_a, K_M, K_O	19.318	0.01
Model 1	k, E_a, K_M, K_O	63.416	3.89e-08
Model 2	k, E_a, K_M, K_O, A_m, B_m	67.579	3.8e-08
Model 3	k_1, k_2, p, E_a, K_M, K_O	65.594	4.38e-08
Model 4	k_1, k_2, p, E_a, K_M, K_O, A_m, B_m	70.412	3.57e-08

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Acknowledgements

First and foremost, I would like to thank my PhD advisor, Dr. Carlos Sierra, for his invaluable guidance and constructive input during my doctoral research. His pursuit of excellence has been a model of a devoted mentor, scholar, and researcher who has encouraged my development as an independent researcher. I would also like to thank him for his undeserved and strained patience, especially for valuable discussions, ideas, advice, general support, and providing a critical and constructive perspective.

I sincerely thank my PhD advisor Georg Guggenberger for his continued interest in my work and his valuable suggestions and insights. He had a significant influence on my becoming a soil scientist.

My special thanks go to the TransTiP team, especially Prof. Antje Schwalb, Dr. Nicole Bröner, Julia Saul, and Alexandra Müller for the great support, the good cooperation, the long and fun days and the fruitful discussions during the last four years. I would like to thank my many colleagues from TransTiP, especially Dr. Felix Nieberding, Dr. Wengang Kang and Dr. Torsten Sachs for their help during fieldwork and research visits in China and Tibet.

I would like to thank all the colleagues at the Max Planck Institute for Biogeochemistry, especially Prof. Susan Trumbore, who hosted me as a PhD student and provided part of the funding for my project, and the staff of the field experiment group, especially Dr. Kübler, Agnes Fastnacht and Nadine Hempel, for their time and patience and the great teamwork that made the whole experiment successful. My special thanks go to Iris Kuhlmann, who never tired of explaining methods, measurements and evaluations to me since I started as a master student at MPI.

I would like to thank all the members of the TEE group, David A. Herrera, Markus Müller, Alison Hoyt, Ingrid Chanca, Estefanía Muñoz, Andrés Tangarife-Escobar, Holger Metzler, and Verónica Ceballos for their support in many ways. Thank you for being my friends in good times and in hard times!

I also want to thank the SIDb development team for the nice cooperation and the super interesting discussions! I have still to publish these results!

Last but not least, I would like to express my deepest appreciation to the love of my life, Soran, for her continuous support, patience and suggestions during and after my PhD. To my family and especially my mother, who are always there for me, talking to me about lack of progress and reminding me that there is more to life than science, which is to have joy in life. You are all wonderful.

I gratefully acknowledge the financial support provided by the German Research Foundation (DFG) within the framework of the International Research Training Group (GRK 2309/1) Geo-ecosystems in Transition on the Tibetan Plateau (TransTiP).

Curriculum Vitae

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List of publications:

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- **Mina Azizi Rad**, Carlos, A Sierra, 2020, “Temperature, moisture and oxygen interaction in a freezing-thawing incubation experiment”, AGU Fall Meeting, Online Everywhere.
- **Mina Azizi Rad**, Aziz Majidi, Mehdi Tehrani, 2014, “The survey of Potassium top dressing and its vertical movement in soil columns”, National Congress of Soil and Environment, Urmia, Iran.