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# Widespread asymmetric response of soil heterotrophic respiration to warming and cooling



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#### HIGHLIGHTS

- Soil heterotrophic respiration (*R*<sub>h</sub>) was measured with a novel experimental mode.
- Widespread asymmetric response of R<sub>h</sub> to temperature warming and cooling was found.
- Soil pH and microbial community explained the widespread asymmetric pattern.
- CO<sub>2</sub> emission will be overestimated by 20% if asymmetric response is not considered.

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#### GRAPHICAL ABSTRACT

Concept diagram of different responses of soil heterotrophic respiration ( $R_h$ ) during warming and cooling phases. (a) Measured data from forest soil in Jiulian; (b) a mode of different  $R_h$  response to warming and cooling. Green shading between red and blue lines represents the difference in  $R_h$  responses to warming and cooling phases ( $\Delta C$ ); diagonal shading represents cumulative C emissions during the cooling phase.



#### ABSTRACT

Soil is the largest organic carbon (C) pool in terrestrial ecosystems. Periodic changes in environmental temperature occur diurnally and seasonally; yet, the response of soil organic matter (SOM) decomposition to varying temperatures remains unclear. In this study, we conducted a modified incubation experiment using soils from 16 forest ecosystems in China with periodically and continuously varying incubation temperature to investigate how heterotrophic respiration ( $R_h$ ) responds to different temperature patterns (both warming and cooling temperature ranging between 5 and 30 °C). Our results showed a pronounced asymmetric response of  $R_h$  to temperature warming and cooling among the soils of all forest ecosystems, with  $R_h$  increasing more rapidly during the warming phase compared to the cooling phase. This asymmetric response of  $R_h$  to warming and cooling temperatures was widespread in all soils. In addition, the amplitude of this asymmetric response differed among different forest ecosystems, with subtropical and warm-temperate forest ecosystems exhibiting greater asymmetric responses. Path analyses showed that soil pH and the microbial community explained most of the variation in this asymmetric response of  $R_h$  to warming and cooling temperatures suggests that accumulated SOM decomposition might be overestimated on average by 20% for

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warming alone when compared with admix warming and cooling. These findings provide new insights on the responses of  $R_h$  to natural shifts in temperature, emphasizing the need to consider this widespread asymmetric response of  $R_h$  to warming and cooling phases to predict C-climate feedback with great accuracy, especially under future non-uniform warming scenarios.

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#### 1. Introduction

Soil heterotrophic respiration  $(R_{\rm h})$  is one of the largest CO<sub>2</sub> fluxes in the global carbon (C) cycle. Therefore, it is possible that relatively small changes in R<sub>b</sub> rates have significant impacts on the global C cycle and climate (Cox et al., 2000; Jones et al., 2003). Of the dozens of variables that regulate  $R_{\rm h}$ , temperature is undoubtedly a major factor influencing  $R_{\rm h}$ and the release of CO<sub>2</sub> (Conant et al., 2011; Schipper et al., 2014; Bracho et al., 2016). The accuracy of quantitative predictions on the C balance between ecosystem C sequestration and decomposition strongly depends on the assumed apparent temperature response  $(Q_{10})$  of  $R_h$  (Conant et al., 2008). In nature, periodic changes in temperature commonly occur diurnally and seasonally (Li et al., 2017). Some researchers have investigated how R<sub>h</sub> responds to increasing temperature and assumed that it responds similarly to decreasing temperature (Xia et al., 2009; Peng et al., 2013). However, this assumption has not been widely examined, and whether  $R_h$  responds equally to both increasing and decreasing temperature might significantly affect modeling results when predicting the feedback between climate change and the C balance.

Several studies on soil respiration have shown that the release of  $CO_2$  is often higher and more rapid during warming versus cooling phases at the diurnal and seasonal scale (Vargas and Allen, 2008; Chen et al., 2017; Li et al., 2017). For example, Li et al. (2017) recently found that  $R_h$  in three alpine grassland soils responds asymmetrically to increasing

and decreasing temperatures, with  $R_h$  rates being significantly higher during the increasing temperature phase than that during the decreasing temperature phase. In addition, field translocation experiments (e.g., transferring ecosystem components to a new site with different climatic conditions to simulate climate warming or cooling) demonstrated that warming and cooling have different influences on ecosystem respiration, indicating that soil microbes might also respond unequally to warming and cooling (Luan et al., 2014; Hu et al., 2016). Despite several independent studies detecting asymmetric responses in soil respiration to warming and cooling temperatures, it remains ambiguous as to whether this asymmetric response is widespread across different terrestrial ecosystems.

Over the last two decades, various studies have attempted to investigate effects of cyclical temperature changes on the decomposition of soil organic matter (SOM) (Fang et al., 2005; Reichstein et al., 2005; Zhu and Cheng, 2011; Xu et al., 2012; Ci et al., 2015). To date, however, the mechanisms regulating how SOM decomposition and soil respiration respond to varying temperatures remain unclear (Xu et al., 2012), significantly limiting the accuracy of predictions on feedback between C balance and climate change. Traditionally, incubation experiments of SOM decomposition in the laboratory were conducted at several different, but constant, temperatures, and were measured at intervals of days, weeks, or months throughout the entire experimental process (Koch et al., 2007; Lefevre et al., 2014). Although useful, this approach does not simulate the realistic scenarios of periodic temperature changes in



Fig. 1. Distribution of the sampling sites in the 16 typical forest ecosystems of China. JF, Jianfeng; XSBN, Xishuangbanna; DH, Dinghu; JL, Jiulian; QYZ, Qianyanzhou; HT, Huitong; GT, Gutian; SJL, Sejila; JY, Jinyun; SN: Shennon; MX, Maoxian; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong.

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