

1 **Nonnegligible role of warming-induced soil drying in regulating warming effect**
2 **on soil respiration**

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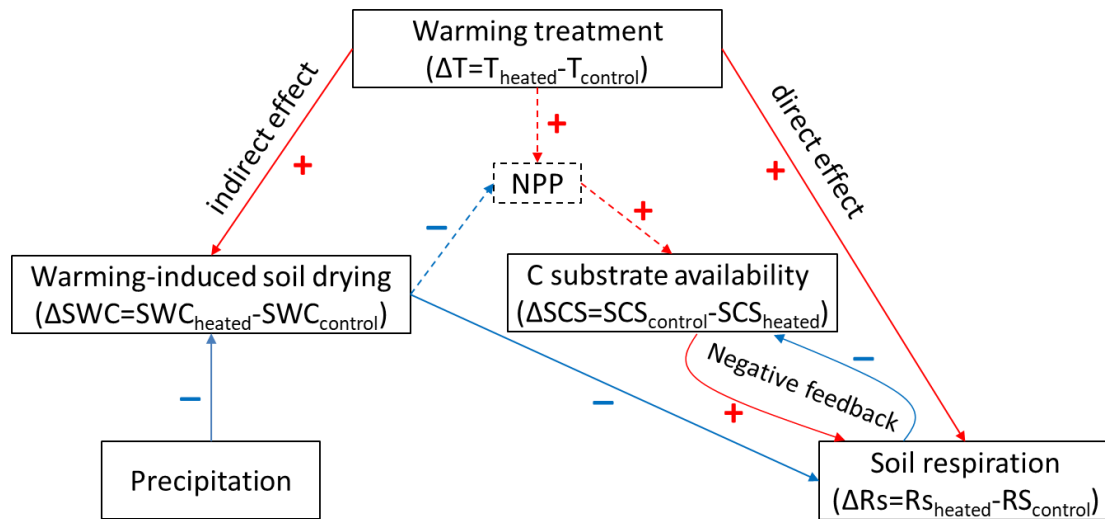
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10 **Abstract**

11 Based on results of a 26-year soil warming experiment (soil temperature being
12 elevated by 5 °C) in a Harvard hardwood forest, Melillo et al. demonstrated a
13 four-phase pattern of long-term warming effect on soil respiration, while the
14 mechanisms were not fully elucidated because they neglected the indirect effect due
15 to warming-induced soil drying. By showing a significant correlation between
16 precipitation anomaly and inter-annual variation of warming effect on soil respiration,
17 we suggest a nonnegligible role of warming-induced soil drying in regulating the
18 long-term warming effect on soil respiration. Our analysis recommends further efforts
19 to consider both the direct and indirect (i.e., warming-induced soil drying) warming
20 effects to gain more in-depth understanding of the long-term soil C dynamics.

21 Understanding the long-term effect of climate warming on soil respiration is a
 22 prerequisite for the projection of future change in global soil carbon (C) pools and
 23 their consequent feedbacks to climate change. Based on results of a 26-year soil
 24 warming experiment (soil temperature being elevated by 5 °C) in a Harvard hardwood
 25 forest, Melillo et al. (1) proposed a hypothesis of four-phase pattern of soil warming
 26 effect on soil respiration ($\Delta R_s = R_{s_{\text{heated}}} - R_{s_{\text{control}}}$) and attributed it to soil substrate
 27 and microbial changes. However, the mechanisms were not fully elucidated because
 28 the authors improperly neglected the indirect effect due to warming-induced decline
 29 in soil moisture (Fig. 1).



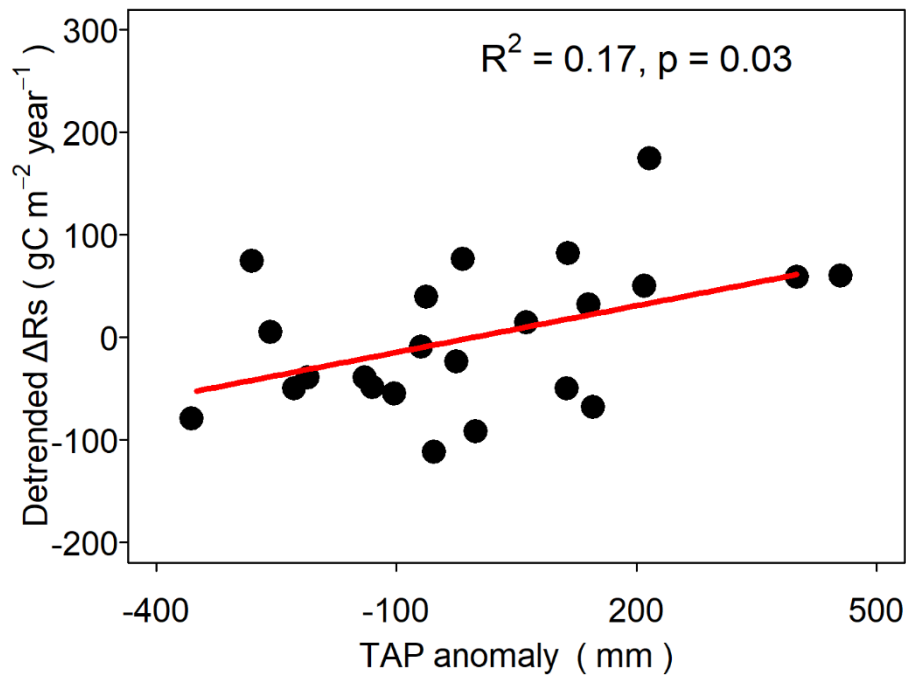
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 31 **Figure 1.** A conceptual framework showing the direct and indirect warming effects on
 32 soil respiration. Precipitation buffers warming-induced soil drying and thus has an
 33 positive effect on inter-annual variation of ΔR_s . Negative feedbacks exist between C
 34 substrate availability and respirational C loss. Current experiment failed to track the
 35 direct and indirect warming effects on forest primary productivity (NPP) and
 36 consequent fresh soil C inputs due to a small plot size (6 x 6 m²) (as indicated by
 37 dashed lines). The symbols “+” in red and “-” in blue indicate positive and negative
 38 effects, respectively.

39

40 Experimental results have evidenced an essential role of soil moisture in
 41 regulating the warming effect on soil respiration (2-5). Lower soil moisture can

42 reduce ΔR_s , and even leads to negative ΔR_s , when soil moisture becomes extremely
43 limiting to plant roots and soil microbial organisms (Fig. 1; 3-6). In addition to the
44 direct warming effect (1), warming-induced soil drying (2-6) may indirectly reduce
45 ΔR_s , especially in drier years (Fig. 1; 2-5). Moreover, soil moisture stress has been
46 evidenced to reduce temperature sensitivity of soil respiration (7, 8).
47 Warming-induced soil drying may have also contributed to a decrease in temperature
48 sensitivity of soil respiration in heated plots, being observed to occur consistently
49 across all four phases during the long-term soil warming experiment in Harvard forest
50 [see Fig. 3 in Melillo et al. (1)]. Unfortunately, we cannot re-analyze the role of
51 warming-induced soil drying due to unavailable soil moisture data (1).

52 As a primary source of soil moisture, precipitation is expected to buffer the soil
53 moisture stress and result in a positive effect on inter-annual variation of ΔR_s (Fig. 1).
54 By retrieving data on total annual precipitation (TAP) anomaly (showing no
55 significant temporal trend, $p=0.94$) and ΔR_s from Melillo et al. (1), we tested the
56 effect of TAP anomaly on inter-annual variation of ΔR_s . As ΔR_s showed a significant
57 decrease over time ($\Delta R_s = -6.1547 \cdot \text{Year} + 12402$, adjusted $R^2 = 0.29$, $p=0.005$) due
58 to long-term microbial C substrate depletion (Fig.1; 1, 9, 10), we thus used detrended
59 (i.e., residual) ΔR_s [being calculated as, measured $\Delta R_{s_i} - (-6.1547 \cdot \text{Year}_i + 12402)$,
60 where i indicates a specific year] to indicate the inter-annual variation of ΔR_s . As
61 expected, we found a significantly positive effect of precipitation anomaly on the
62 inter-annual variation of ΔR_s (slope = $0.15 \text{ g C m}^{-2} \text{ year}^{-1}$ per mm; adjusted $R^2=0.17$,
63 $p=0.03$; Fig. 2). Our result suggests a significant role of soil moisture in regulating the
64 warming effect on soil respiration. It further implies that warming-induced soil drying
65 stress has very likely exerted a negative effect on the response of soil respiration to
66 long-term warming treatment in Harvard forest.



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68 **Figure 2.** Significant effect of total annual precipitation (TAP) anomaly (mm) on the
69 inter-annual variation of warming-induced ΔR_s ($\text{g C m}^{-2} \text{ year}^{-1}$). Because ΔR_s
70 showed a significant decrease over time ($\Delta R_s = -6.1547 \cdot \text{Year} + 12402$, adjusted $R^2 =$
71 0.29 , $p=0.005$) due to soil C substrate depletion, we used detrended residual [being
72 calculated as, measured $\Delta R_{s_i} - (-6.1547 \cdot \text{Year}_i + 12402)$, where i indicates a specific
73 year] to indicate the inter-annual variation of ΔR_s . Note that our analysis excluded
74 data for the years 1995, 2005, 2010 due to warming system failure.

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76 The long-term experiment, with each plot covering a small area of $6 \times 6 \text{ m}^2$ (1),
77 generally represented a scenario of soil C depletion under soil warming, while it failed
78 to demonstrate the story in a whole C cycle perspective. The small plot size was not
79 able to track the direct and indirect (i.e., warming-induced soil drying) warming
80 effects on forest primary productivity (Fig. 1), which could consequently provide
81 fresh C substrates for soil respiration (11). In that case, negative feedbacks between C
82 substrate limitation and respirational C loss likely dominate a long-term reduction of
83 ΔR_s (9, 10). By inducing a reduction of soil moisture (2-6, 12, 13), soil warming also
84 indirectly regulates ΔR_s via inducing changes in the composition and activity of

85 microbial community (5, 14). For instance, warming-induced soil moisture stress may
86 have contributed substantially to the declining trends of ΔR_s during the relatively drier
87 periods 1997-2002 and 2015-2016 [see Fig. S2 in Melillo et al. (1)].

88 As the indirect effect due to warming-induced soil drying stress has not been
89 addressed properly, the mechanisms of the four-stage pattern of long-term warming
90 effect on soil respiration are likely not fully elucidated (1). Moreover, Melillo et al. (1)
91 assumed that microbial respiration accounted for a constant proportion
92 (approximately 2/3) of soil respiration, while they ignored temporal changes in the
93 microbial proportion over the four-phase pattern of soil respiration. Therefore,
94 in-depth understanding of the long-term warming effect on soil C dynamics calls for
95 further efforts to consider both the direct and indirect (i.e., warming-induced soil
96 drying) effects in a whole C cycle perspective at an ecosystem scale.

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98 **Acknowledgements:** This work was supported by the National Natural Science
99 Foundation of China (Nos. 41630750 & 31400381) and State Key Laboratory of
100 Earth Surface and Resource Ecology (No. 2017-ZY-07).

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