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Legacy effect of constant and diurnally oscillating temperatures on soil respiration and microbial community structure

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Abstract

Laboratory incubation studies evaluating the temperature sensitivity of soil respiration often use measurements of respiration taken at a constant incubation temperature from soil that has been pre-incubated at the same constant temperature. However, such constant temperature incubations do not represent the field situation where soils undergo diurnal temperature oscillations. We investigated the legacy effects of constant and diurnally oscillating temperatures on soil respiration and soil microbial community composition. A grassland soil from the United Kingdom was either incubated at a constant temperature of 5°C, 10°C, or 15°C, or diurnally oscillated between 5°C and 15°C. Soil CO_2 flux was measured by temporarily moving incubated soils from each of the above-mentioned treatments to 5°C, 10°C or 15°C, such that soils incubated under every temperature regime had CO_2 flux measured at each temperature. We hypothesised that, irrespective of measurement temperature, CO_2 emitted from the 5°C to 15°C oscillating incubation would be most like the soil incubated at 10°C. The results showed that both incubation and measurement temperatures separately influence soil respiration. Oscillations between 5°C and 15°C resulted in significantly greater CO_2 flux than constant incubations at 10°C or 5°C but were not significantly different from the 15°C incubation. The greater CO_2 flux from soils previously incubated at 15°C, or oscillating between 5°C and 15°C, coincided with a depletion of dissolved organic carbon and a shift in the phospholipid fatty acid profile of the soil microbial community, consistent with stress associated with substrate depletion and microbial starvation when incubated at higher temperatures. Our results suggest that daily maximum temperatures are more important than daily minimum or daily average temperatures when considering the response of soil respiration to the diurnally asymmetric warming that is expected to occur as a result of climate change.

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KEYWORDS
climate change, diurnal temperature range, soil microbial community, soil organic carbon, soil respiration

1 | INTRODUCTION

Soils harbour the largest actively cycling pool in the carbon cycle (Harden et al., 2018). Depletion of soil organic matter releases CO_2, a greenhouse gas, into the atmosphere, contributing to global warming. The resulting increase in global temperatures is expected to stimulate heterotrophic soil respiration (Bardgett et al., 2008; Walker et al., 2018), thus causing a positive feedback that releases more CO_2 into the atmosphere. The annual release of CO_2 from soils by heterotrophic microorganisms is about 8–9 times higher than anthropogenic emissions from the burning of fossil fuels (Dutta & Dutta, 2016), so reducing the uncertainty concerning the magnitude of the positive feedback under future climate change scenarios deserves attention (Davidson & Janssens, 2006).

The temperature sensitivity of soil respiration is often characterised by a fixed Q_{10} value that represents the increase in soil respiration that occurs after a 10°C increase in mean soil temperature (Meyer et al., 2018). However, a Q_{10} value generated from the incubation of soil samples in the laboratory at constant temperatures fails to consider the extent to which soil temperature oscillates diurnally, the influence that the legacy these oscillations may have on the inherent temperature sensitivity of soil respiration, or whether average temperatures are adequate to capture the temperature response of soil respiration to the changes in temperature that we actually expect soils to experience (Mitra et al., 2019). There is a lack of experimental evidence highlighting the importance of diurnal temperature range, daily maximum temperature or daily minimum temperature on soil respiration. This knowledge gap is important because, along with a future increase in global mean temperatures, we also expect a future dampening of the diurnal temperature range, with daily minimum temperatures expected to increase more than daily maximum temperatures (Braganza et al., 2004).

Oscillating temperatures are uncommon in laboratory experiments, where soils are often incubated under constant temperatures for several months (von Lützow & Kögel-Knabner, 2009; Yan et al., 2017). Diurnal variation in the rates of soil microbial functions that release atmospheric gases such as CO_2, N_2O and CH_4 have been reported in both field (Zhou et al., 2015) and laboratory (Xu et al., 2016) studies. Such diurnal variation has been attributed largely to temperature oscillations (Shurpali et al., 2016). In addition to the direct impacts of temperature on soil respiration that are due to increases in the activity of soil microbial communities, indirect effects on microbial activity could occur due to long-term shifts in soil microbial community composition as a result of thermal adaptation (Luo et al. 2001; Davidson et al., 2006; Bradford et al. 2008; Bradford et al., 2010; Buysse et al. 2013). Understanding how the legacy effects of changes in temperature regimes influence the structure and function of soil microbial communities is currently among the most important areas of investigation in the field of microbial ecology (Antwis et al., 2017). Under future diurnally asymmetric warming, soil microorganisms may become thermally adapted to a narrower diurnal temperature range and respond differently to temperature increases than the communities that currently inhabit soils.

Measuring soil respiration in soils that are incubated at a diurnally oscillated temperature may create conditions that are more similar to those experienced by soil microbial communities in nature (Thiessen et al., 2013). However, previous attempts at measuring soil respiration under controlled oscillating temperatures are rare. A few studies have achieved this simulated oscillation by moving soils from one temperature to another and holding them at these constant temperatures for longer than may occur naturally (e.g., between 9 and 12 h), during which soil respiration measurements were made (e.g., Fang et al., 2005; Thiessen et al., 2013). Unfortunately, these studies did not report how microbial community composition changed as a result of these oscillating soil temperatures. Past temperature regimes already experienced by soil can influence both the soil microbial community (Wu et al., 2010) and substrate availability (Pold et al., 2017). It is uncertain how the temperature sensitivity of respiration responds to changes in soil microbial community and substrate depletion due to the legacy effect of a previous temperature regime. Comparing the soil microbial community composition and its function ex situ under both constant and diurnally oscillating temperatures that mimic real diurnal temperature oscillations may offer a better understanding of how soil microbial communities may change under future environmental change and help us to better predict the magnitude of the positive feedback of CO_2 flux into the atmosphere.

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We designed and executed a laboratory incubation experiment to examine the effects of constant and diurnally oscillating temperatures on soil microbial community structure and function. The temperature treatments were chosen to reflect average daily minimum, daily average and daily maximum temperatures in Reading, United Kingdom measured over 28 years. Soils were incubated at these three constant temperatures (5°C, 10°C or 15°C) alongside soils that were oscillated between average daily minimum (5°C) and daily maximum (15°C) temperatures. Soil CO_2 flux was measured by temporarily moving incubated soils from the above-mentioned treatments to 5°C, 10°C or 15°C, such that soils incubated at each temperature had CO_2 flux measured at every temperature. Our approach used incubation and measurement temperatures as statistical factors to explore the influence of incubation temperature on respiration at the measured temperature. Our aim was to determine whether soil samples previously incubated under different temperature regimes exhibit different respiration rates, even if the measurements of respiration are all made at the same temperature. We hypothesised that (1) respiration measurements made at higher temperatures would result in greater respiration rates, (2) incubation temperature would induce changes in soil microbial community structure and the availability of soil car C and N, and that (3) these changes in community composition and biogeochemistry would lead to different respiration rates from soils incubated under different temperature regimes, even when respiration was measured at the same temperature. Our null hypothesis was that respiration of soils with a legacy of diurnally oscillating between 5°C and 15°C would be similar to respiration from soils previously incubated at 10°C.

2 | MATERIALS AND METHODS

2.1 | Site selection and soil sampling

Soil was collected at 0–10 cm depth from a permanent grassland field (Latitude 51°28.564′, Longitude 000 °54.198′) on the University of Reading experimental farm at Sonning, United Kingdom. The soil was identified as a Chromic Endoskeletic Luvisol. Details of the soil description and land use history are provided in Adekanmbi et al. (2020). Multiple subsamples from an area of approximately 10 m^2 were bulked together. The fresh soil was sieved to 4 mm and thoroughly mixed to obtain a single homogenous composite sample. We previously demonstrated that sieving soil collected from the same location to 4 mm did not significantly influence CO_2 flux (Adekanmbi et al., 2020). The homogeneous composite sample was stored at 4°C until the start of the experiment

TABLE 1 Physical and chemical properties of the soil used in the experiment

Parameters	Values
%Sand	46.8
%Silt	45.0
%Clay	8.2
Texture	Loam
%WHC*	43.6
pH in water	6.52
Total N (g^{-1} kg^{-1} soil)	2.53
Total (C g^{-1} kg^{-1} soil)	26.4
C/N ratio	10.4
NH_4^+ (mg^{-1} kg^{-1} soil)	0.53
NO_3^- (mg^{-1} kg^{-1} soil)	57.3
Total extractable N (mg^{-1} kg^{-1} soil)	57.8

[a]WHC, water-holding capacity.

where subsamples were randomly assigned to treatments. A subsample of approximately 500 g was used to characterise the soil. Available NO_3^- and NH_4^+ were immediately analysed on the fresh soil and the remainder air-dried to characterise soil texture, water-holding capacity (%WHC), pH in water, total carbon (TC), and total nitrogen (TN) (Table 1). The methods for each of these analyses are reported in the Supporting Information.

2.2 | Experimental design

The experiment was a 4 × 3 factorial design comprising four incubation temperature regimes (5°C, 10°C, 15°C, or diurnally oscillating between 5°C and 15°C) and three measurement temperatures (5°C, 10°C and 15°C), with four replicates (Table S1), resulting in 12 treatments and 48 units (Treatments 1–12 in Table S2). Sub-samples of the homogenous composite soil sample collected from the field were randomly assigned to treatments. Each week of the experiment the soil samples were incubated in controlled environment chambers for 6 days at their allocated incubation temperature regimes before moving to their allocated measurement temperatures 24 h prior to respiration measurement, and then returned to their allocated incubation temperature after measurement of CO_2 flux (Figure 1a, b). Our preliminary measurements indicated that 24 h was sufficient for the temperature in the soil to equilibrate with the chamber temperature. Two blank (without soil) incubation jars were incubated at each measurement temperature as a blank to correct for background atmospheric CO_2 concentration in the mesocosms and accounted for while calculating the CO_2 flux.

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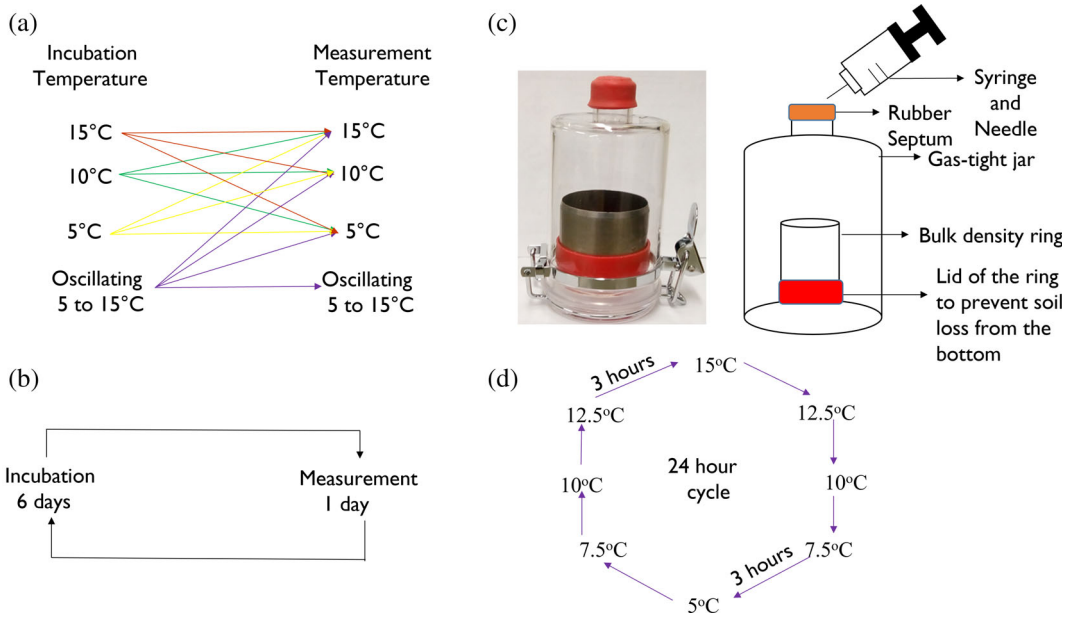

FIGURE 1 Experimental design including (a) a graphical depiction of the experimental treatments showing how individual treatments were moved from their incubation temperature to their measurement temperature prior to CO_2 flux measurements; (b) the weekly schedule for moving soils from their incubation temperatures to their measurement temperatures; (c) the design of the incubation containers and the method by which headspace gas samples were collected from the soil incubation containers; and (d) the daily temperature regime that the soils assigned to the 5°C–15°C oscillating treatment were exposed to, with the temperature held for 3 h at each temperature step

Four extra cores were both incubated and measured in an environment of diurnally oscillating temperature between 5°C and 15°C (See treatment 13 in Table S1). Measurements of CO_2 flux were made when the environment was at 10°C while the temperature was decreasing during the diurnal oscillation. The addition of this treatment meant that, at the end of the experiment, we had soils that had remained (without movement) at 5°C, 10°C, 15°C and diurnally oscillating between 5°C and 15°C (representing 4 treatments and 16 experimental units). These units were used for post-incubation soil chemical and biological analysis.

2.3 | Experimental set-up and CO_2 flux measurements

Field moist soil samples of 70 g fresh weight (equivalent to 56.51 g dry weight) were weighed into a 5 × 5 cm cylinder (height × diameter; volume = 98.22 cm^3) and placed in a 320 ml gas-tight container (Figure 1c). The containers were modified to allow gas collection ports, which were covered with Parafilm to reduce moisture loss (but allow gas exchange) when not in use, following Adekanmbi et al. (2020). The soils were adjusted to 60% of their water-holding capacity, as described by Yang et al. (2017). All the soil samples were pre-incubated for 7 days at their respective incubation temperature to allow the sieving/re-wetting induced flush in respiration (Liu et al., 2018) to subside before the first CO_2 flux measurement was made. The temperatures selected for our experiment were the average daily minimum (5°C), average daily maximum (15°C) and average daily mean (10°C) temperatures measured over a 28-year (January 1, 1990–May 2018) period at the University of Reading Meteorological station, situated approximately 2.5 miles from University of Reading experimental farm at Sonning, where the soil for this experiment was collected. We set the oscillating treatment to oscillate diurnally between 5°C and 15°C by programming a growth chamber to spend 3 h at each of eight temperatures per day (5°C, to 7.5°C, to 10°C, to 12.5°C, to 15°C, to 12.5°C, to 10°C, to 7.5°C, and then back to 5°C), as shown in Figure 1d.

The experiment lasted for 119 days (17 weeks). Soil respiration was measured as CO_2 flux every week up until the third week (day 21) and then at two-week intervals thereafter until the 17th week. Prior to each CO_2 flux measurement, the Parafilm® was removed to allow the gas in the gas-tight container to mix with the atmosphere. During CO_2 flux measurement, containers were sealed with a Suba-Seal septa and kept at the measurement temperature for 1 h before a 15 ml headspace gas sample was taken from each container using a syringe and hypodermic needle and transferred into a pre-evacuated ***Labco exetainer*** vial. After each sampling, the septum was removed and the Parafilm replaced to reduce moisture

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loss. The gas samples were analysed using an Agilent 7890A (Agilent Technologies, Wilmington) gas chromatograph fitted with a 1/8 inch stainless steel packed column (HayeSep Q 80/100) to separate the CO_2 peak in an oven held at 60°C using N_2 as the carrier gas at a rate of 21 ml min^{-1} prior to conversion to CH_4 in a methanizer and detection using a flame ionisation detector. The moisture content of the soil in each container was adjusted back to 60% of their water-holding capacity after collecting gas and before returning samples back to their incubation temperatures by addition of deionised water to compensate for mass loss due to evaporation.

2.4 | Laboratory analysis of soil chemical and biological properties

At the end of the experiment (after 17 weeks), soil samples were taken from the 16 containers that had remained (without movement) at 5°C, 10°C, 15°C, or diurnally oscillating between 5°C and 15°C for the entirety of the experiment to examine soil chemical and biological properties. A 10 g sub-sample of soil was extracted immediately for determination of available NO_3^- and NH_4^+. A further 5 g was used to determine the gravimetric water content and adjust the results of the NO_3^- and NH_4^+ analysis for soil moisture so that they could be expressed on a dry mass basis. A 15 g sub-sample was air-dried for chemical analysis to determine TC, TN, and hot and cold water extractable carbon (HWEOC and CWEOC). A 5 g sub-sample was freeze-dried prior to phospholipid fatty acid (PLFA) analysis. Individual fatty acid biomarkers were assigned to microbial groups, as described in Table S2, and used to calculate metrics that are indicators of microbial stress. The methods for each of these analyses are reported in the Supporting Information.

2.5 | Statistical analysis

Differences in soil respiration due to incubation and measurement temperatures over the period of 17 weeks were tested in Genstat (10th edition) using repeated measures analysis of variance (ANOVA) and Fisher's least significant difference (LSD) test was used for pairwise comparisons. Repeated measures ANOVA was selected because multiple measurements on the same sample are not independent. Non-metric multi-dimensional scaling (NMDS) ordination derived from Bray–Curtis similarities was used to separate soil microbial community structures of samples subjected to different incubation temperatures using the *vegan* package (Oksanen, 2017) in R v3.5.1 (R Development Core Team, 2018). The Bray–Curtis distance, performed in two dimensions, had a stress factor of 0.052. PERMANOVA was used to assess whether incubation temperature influenced the soil microbial community distance. One-way ANOVA was also used to assess the differences in the NMDS 1 and 2 after establishing that there was a significant difference in community distance due to temperature to examine the direction of temperature impact on soil microbial community. One-way ANOVA was used to test the differences in soil properties and PLFA biomarkers due to incubation temperatures.

3 | RESULTS

3.1 | Effects of measurement and incubation temperatures on soil CO_2 flux

The CO_2 flux data for each individual treatment are presented in Figures S1 and S2 of the Supporting Information. Both incubation ($p < 0.001$) and measurement ($p < 0.001$) temperature had a significant effect on the CO_2 flux measured (Table 2). However, there was no significant interaction between incubation and measurement temperatures ($p = 0.680$). Irrespective of measurement temperature, incubating soil at 15°C, or oscillating between 5°C and 15°C, released significantly ($p < 0.05$) more CO_2 than incubating at 5°C or 10°C (Figure 2a, Table 2). As expected, CO_2 flux, when measured at 15°C, was significantly ($p < 0.05$) greater than CO_2 flux measured at 5°C or 10°C (Figure 2b, Table 2). However, counter to expectations, it was observed that soils measured at 5°C released slightly (but not significantly; $p > 0.05$) more CO_2 compared with soils incubated at 10°C (Figure 2b). Irrespective of measurement temperature, CO_2 flux from the soils that

TABLE 2 Summary table for two-way repeated measures ANOVA for soil respiration; incubation and measurement temperatures were the main (subject) factors

Source	*df*	*F* value	*p* value
Incubation temperature (I)	3	9.21	**0.001**
Measurements temperature (M)	2	9.01	**0.001**
Incubation week (W)	9	12.54	**0.001**
I × M	6	0.66	0.680
W × I	27	3.81	**0.001**
W × M	18	3.43	**0.001**
W × I × M	54	1.25	0.180

Note: Values in bold letters are significantly different at $p < 0.01$.

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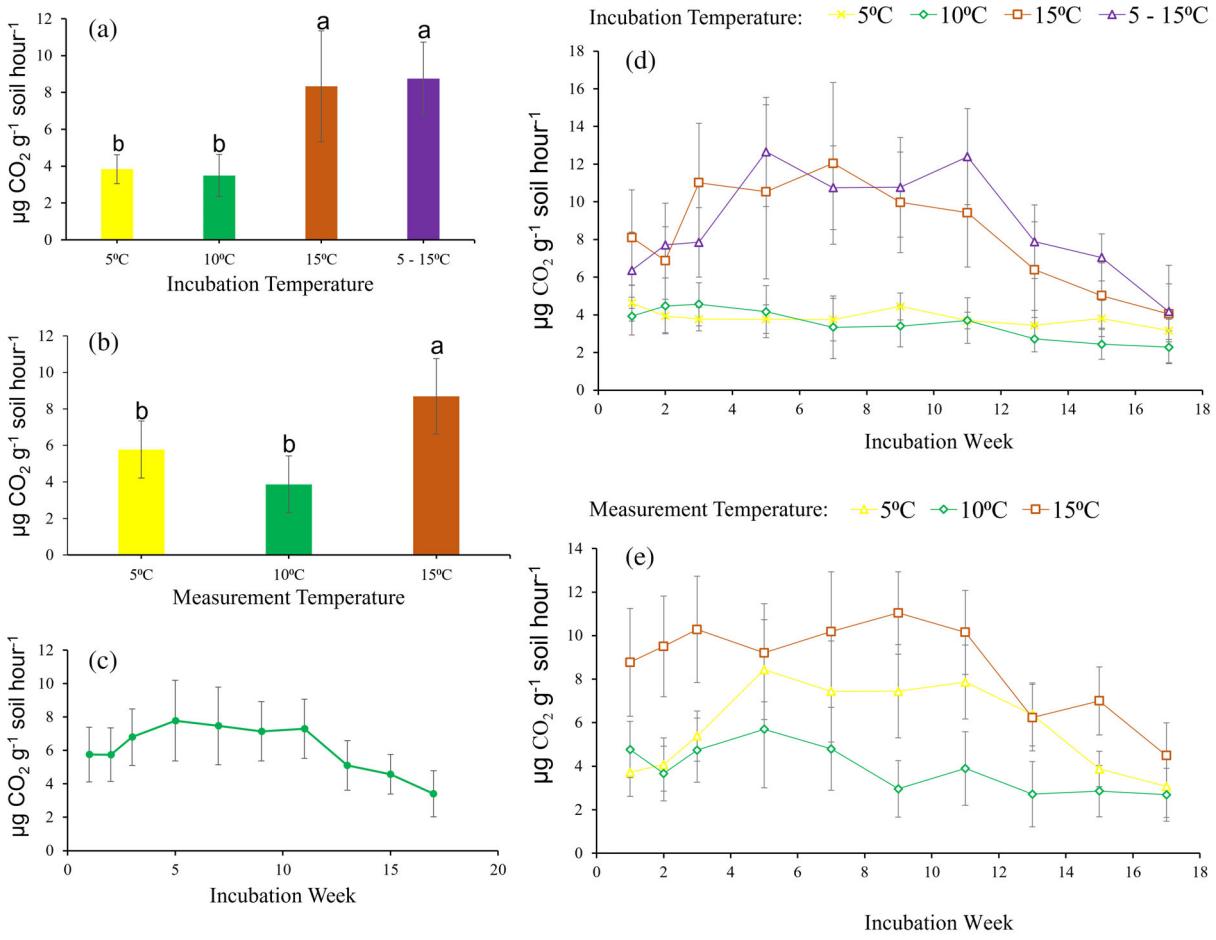

FIGURE 2 Effects of (a) incubation temperature on soil CO_2 flux, regardless of measurement temperature or week, (b) measurement temperature on soil CO_2 flux, regardless of incubation temperature or week, (c) incubation week on soil CO_2 flux, regardless of incubation temperature or measurement temperature, (d) incubation temperature on soil CO_2 flux each week, regardless of measurement temperature, and (e) measurement temperature on soil CO_2 flux each week, regardless of incubation temperature. Error bars represent standard errors of the mean. Bars with the same lower case letters are not significantly different from each other ($p > 0.05$). For (a) $n = 120$, for (b) $n = 160$, for (c) $n = 48$, for (d) $n = 12$ and for (e) $n = 16$

oscillated between 5°C and 15°C was not significantly different ($p > 0.05$) from the soils incubated at 15°C.

Incubation week had a significant ($p < 0.001$) effect on the CO_2 flux measured (Table 2), as indicated by a slightly elevated CO_2 flux measured in the middle of the incubation (Week 3 to Week 11) (Figure 2c). There was also a significant interaction ($p < 0.001$) between incubation week and incubation temperature, and between incubation week and measurement temperature on soil CO_2 flux (Figure 2d, e, Table 2). The elevated CO_2 flux measured in the middle of the incubation (Week 3 to Week 11) was more pronounced in treatments incubated at 15°C or oscillating between 5°C and 15°C (Figure 2d). Although CO_2 flux measured at 5°C was lower than that measured at 10°C in Week 1 of the experiment, it was greater in soils measured at 5°C for the remainder of the experiment (Figure 2e).

3.2 | Effects of incubation temperature on soil carbon and nitrogen

Total and dissolved C generally decreased and total and dissolved N generally decreased with increasing incubation temperature in soils from the 16 experimental units that remained (without movement) under the same temperature regime for the duration of the experiment (Figure 3; Table S1). CWEOC (Figure 3a; Table S3) was significantly ($p < 0.05$) higher in soils incubated at 5°C and 10°C compared with those incubated at 15°C or oscillated between 5°C and 15°C. Furthermore, soils incubated at 5°C had a significantly ($p < 0.05$) higher HWEOC than all other incubation temperatures (Figure 3b; Table S3). TC (Figure 3c; Table S3) was significantly ($p < 0.05$) higher in soils incubated at 5°C or 10°C, compared with those incubated at 15°C or oscillated between 5°C and 15°C. Total extractable

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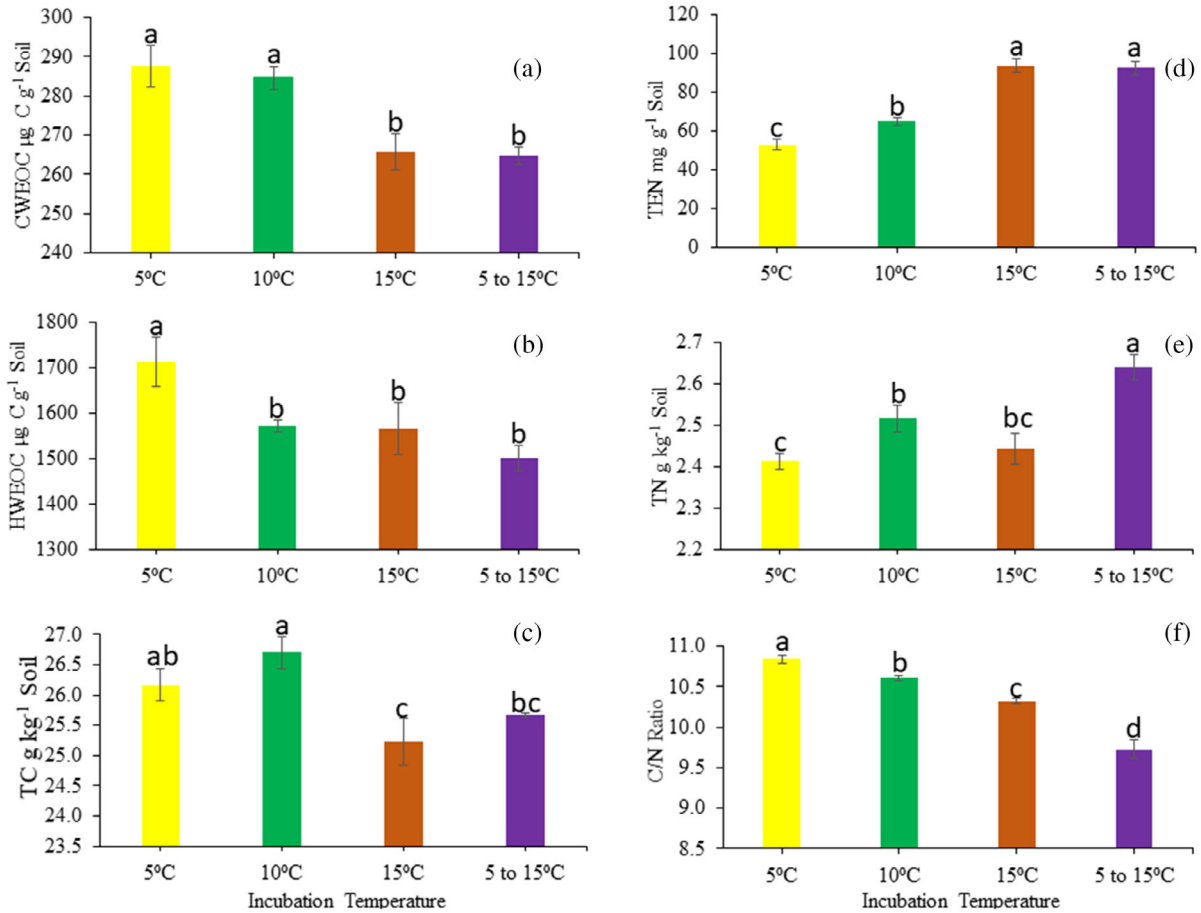

FIGURE 3 Influence of incubation temperature on cold (CWEOC = a) and hot (HWEOC = b) water extractable carbon, Total carbon (TC = c), total extractable N (NH_4^+ and NO_3^-) (TEN = d), total nitrogen (TN = e) and C/N ratio (f). Bars and error bars represent mean and standard error of the mean of treatments ($n = 4$) where each replicate soil sample was exposed (without movement) to the same incubation and measurement temperature. Bars that share the same letter within a graph are not significantly different from each other ($p > 0.05$)

N (TEN) significantly ($p < 0.05$) increased with incubation temperature (Figure 3d; Table S3). Soils oscillated between 5°C and 15°C had a similar TEN to soils incubated 15 °C, but significantly ($p < 0.05$) greater than soils incubated at 5°C or 10°C. The TN concentration was significantly ($p < 0.05$) greater in soils oscillated between 5°C and 15°C, compared with all other treatments incubated at constant temperatures (Figure 3e; Table S3). The C/N ratio significantly ($p < 0.05$) decreased with increasing incubation temperature, but, unlike TEN, soils oscillated between 5°C and 15°C had a significantly ($p < 0.05$) different (lower) C/N ratio than soils incubated at 15°C (Figure 3f; Table S3).

3.3 | Impacts of incubation temperature on soil microbial community composition

The structure of the soil microbial community, measured using PLFA biomarkers, was affected by soil incubation temperature, as shown in Figure 4. Temperature had a significant ($p = 0.002$) effect on microbial community distance (Bray–Curtis distance between the PLFA profiles). One-way ANOVA of NMDS score 1 (NMDS1) showed that the soil microbial community structure in soils incubated at 5°C and 10°C was not statistically different from one another, but were distinct ($p = 0.0001$) from those in soils incubated at 15°C or oscillated between 5°C and 15°C (Figure 5, Table S4). There was slightly (non-significant; $p > 0.05$) lower abundance of bacteria and total PLFA (i.e., total microbial biomass) in soils incubated at 15°C, or oscillated between 5°C and 15°C, compared with soils incubated at 5°C or 10°C (Figure 5a, b). Incubation temperature also had a significant effect on PLFA biomarkers potentially indicative of microbial stress (Figure 5). The abundance of fungal biomarkers and the fungal/bacterial ratio was significantly ($p < 0.05$) lower in soils incubated at 15°C or oscillated between 5°C and 15°C, compared with soils incubated at

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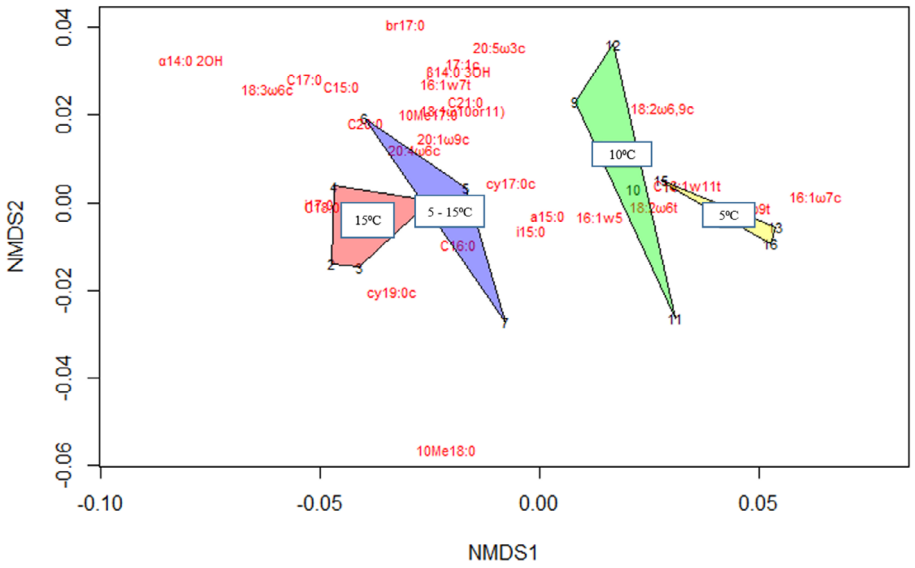

FIGURE 4 Non-metric multi-dimensional scaling (NMDS) plot showing the distribution of lipid biomarkers as influenced by soil incubation temperature on the soil microbial community structure measured using phospholipid fatty acid (PLFA) analysis. The PLFA biomarkers with the most positive or most negative values on NMDS1 are responsible for the separation of the samples incubated at different temperature regimes. The distance is Bray–Curtis, performed in two dimensions, with a stress factor of 0.054. Shaded coloured regions encompass samples from treatments with different incubation temperatures ($n = 4$) where each replicate soil sample was exposed (without movement) to the same incubation and measurement temperature regime

5°C or 10°C (Figure 5d, e). Furthermore, the ratio of Gram-negative/Gram-positive bacteria was significantly ($p < 0.05$) greater in soils incubated at 5 or 10°C compared with soils incubated at 15°C or oscillating between 5°C and 15°C (Figure 5c; Table S4). Likewise, the ratios of (i) cis to trans isomers, (ii) iso to anteiso branching and (iii) cyclopropyl fatty acids to their monoenoic precursors were all significantly ($p < 0.05$) higher in soils incubated at 15°C or oscillating between 5°C and 15°C, compared with those incubated at 5°C or 10°C (Figure 5f, g and h; Table S4).

4 | DISCUSSION

4.1 | The legacy of previous incubation temperature regime on soil respiration

It is well established in multiple soil warming experiments undertaken in the field and laboratory that soil respiration increases in response to temperature increases (von Lützow & Kögel-Knabner, 2009; Bell et al., 2010; Karhu et al. 2014; Carey et al. 2016; Melillo et al., 2017). Faster metabolism of microbially available organic carbon is the major reason suggested for the increases in soil CO_2 flux observed (Melillo et al., 2017; Walker et al., 2018; Zogg et al., 1997). Overall, we found that, regardless of measurement temperature, CO_2 flux was greater from soils that had previously been incubated constantly at 15°C (representing the daily maximum temperature) compared with 5°C (representing daily minimum temperature) (Figure 2a). Our observation implies that the temperature that a soil has previously been exposed to, even for just a short period of time (i.e., days and weeks rather than years and decades), to can exert a considerable legacy effect on the future soil respiration rate.

We observed similar CO_2 flux from soils that were incubated constantly at 15 °C and soils incubated at diurnally oscillating soil temperature between 5°C and 15°C (Figure 2a). This observation counters our null hypothesis that respiration of soils diurnally oscillating between 5°C and 15°C would be similar to respiration from soils incubated at 10°C. To explain this observation, we propose that the time spent at 15°C in the diurnally oscillating treatment was sufficient for soil microbial communities to produce extracellular enzymes to depolymerise enough macromolecules to prevent the availability of low molecular weight compounds from being the factor limiting the rate of intracellular respiration. If our explanation is correct, then it implies that daily maximum temperature is an important factor influencing the transformation of soil organic carbon to CO_2; perhaps more important than daily mean temperature. This assertion has important implications for our predictions of the effect that future environmental change may have on the

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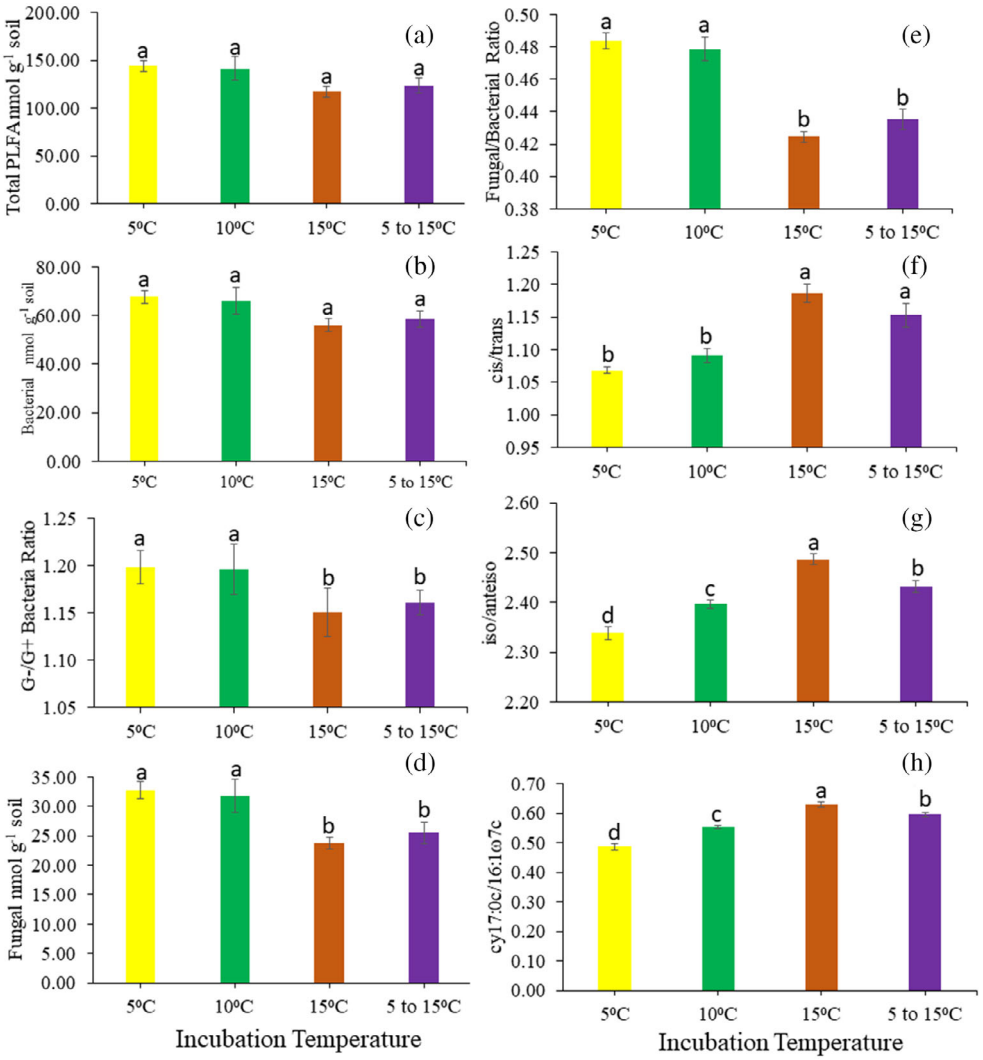

FIGURE 5 Influence of incubation temperature on a range of metrics derived from phospholipid fatty acid (PLFA) analysis that are often used as indicators of microbial stress. Metrics are total PLFA (a), bacterial abundance (b), Gram-negative/Gram-positive bacterial ratio (G−/G+) (c), fungal abundance (d), fungal/bacterial ratio (e) cis/trans isomer ratio (f), iso/anteiso branching ratio (g) and cyclpropyl to monoenoic precursor (cy17:0c/16:1ω7c) ratio (h). Bars and error bars represent mean and standard error of the mean of treatments ($n = 4$) where each replicate soil sample was exposed (without movement) to the same incubation and measurement temperature. Bars that share a letter are not significantly different from one another ($p < 0.05$)

global carbon cycle. The last half of the 20th century saw daily minimum temperatures increase by 0.9 °C while daily maximum temperatures increased by only 0.6°C (Braganza et al., 2004). Therefore, while the climate warms, we are experiencing a reduction in the diurnal temperature range (Alexander et al., 2006) due to increased cloud cover and sulphate aerosol emission (Hansen et al., 1995). Therefore, models that simulate the temperature sensitivity of respiration based on observations made in laboratory incubations at constant temperatures (e.g., Q_{10} values) may fail to adequately capture the impact of asymmetric warming on soil respiration. For example, a 1°C increase in daily mean temperature will likely equate to a less than 1°C increase in daily maximum temperature and so assuming symmetrical warming may overestimate the impact of climate change on soil respiration. It is thus imperative to ensure that the next generation of land-surface models adequately simulate the impact of this diurnally asymmetric warming on the production and activity of extracellular enzymes and the subsequent impacts on soil heterotrophic respiration.

4.2 | Shifts in the soil microbial community structure in response to temperature regimes

An explanation for our observations regarding the legacy of prior incubation temperature on soil respiration is that the soil microbial community could have shifted in response to the temperatures that they were incubated at, as reported by Bradford et al. (2010). It is clear from global datasets of soil microbial communities that lower soil respiration at lower temperatures is indicative of the development of soil microbial communities with slower metabolic activities, such as fungi (Crowther et al., 2019), leading to the accumulation of organic carbon in fungal dominated ecosystems in colder climates. Along with higher rates of soil respiration, we observed a shift away

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from a fungal dominated microbial community to one dominated more by Gram-positive bacteria in soils incubated at a higher (or diurnally oscillating) temperature (Figure 5). This shift is consistent with observations made a 12 years of warming conditions in the field (Frey et al., 2008). Our results therefore lend support to the general hypothesis that soils with a lower fungal-to-bacterial ratio have a lower potential to accumulate soil organic matter due to lower carbon use efficiency (Bonner et al., 2018; Malik et al., 2016). Greater dominance of fungi and Gram-negative bacteria has also been observed in soils with more total and labile carbon (Fanin et al., 2019; Whitaker et al., 2014). Therefore, the presence of greater total, and hot and cold water extractable organic carbon that we observed in soils incubated at lower temperatures (Figure 3) may have caused, or been the result of, shifts in the soil microbial community that raised the fungal-to-bacterial ratio and Gram-negative-to-Gram-positive bacteria ratio and may constitute an indirect mechanism by which soils respond to changes in temperature. These observations lend support to our hypotheses that incubation temperature will induce changes in soil microbial community structure and the availability of soil C and N, and that these changes in community composition and biogeochemistry would lead to different respiration rates from soils incubated under different temperature regimes, even when respiration was measured at the same temperature.

4.3 | Depletion of soil organic matter at higher or oscillating incubation temperatures

Walker et al. (2018) identified a role for both substrate depletion and a permanent acceleration in microbial physiology that leads to faster respiration, growth and turnover in warmed soils. Like Zogg et al. (1997), we observed differences in soil microbial community composition (Figure 5) between soils incubated at different temperatures that correspond with substrate depletion and soil respiration. Our laboratory incubation experiment revealed elevated soil CO_2 flux between Week 5 and Week 11, after which CO_2 flux then decreased over time. This observation can most plausibly be explained by depletion of the labile soil organic carbon supply after 11 weeks. This explanation is consistent with the results from You et al. (2019), who observed a decrease in soil CO_2 flux due to increasing temperature towards the end of a 35-day soil incubation study.

The lower concentration of CWEOC (Figure 3a) measured in soils incubated constantly at 15°C or diurnally oscillated between 5°C and 15°C reveals that these soils have been depleted of dissolved organic carbon (DOC). This observation supports the results of Bertolet et al. (2018) who reported lower DOC under warmer temperatures in a 28-day incubation study. In another short-term experiment, it was reported that increasing temperature reduced the DOC and microbial biomass carbon without any significant changes in soil organic matter or total C (You et al., 2019). In this study, we found higher DOC in soils incubated at 5°C and 10°C, compared with those incubated at 15°C or oscillated between 5°C and 15°C. This observation indicates that a similar rate of substrate depletion occurred in soils incubated constantly at a high temperature and soils that oscillated between high and low temperatures. Our findings therefore imply that daily maximum temperature plays a more important role in soil organic matter (de)stabilisation than daily mean temperatures, complementing our interpretation of the CO_2 flux measurements. The notion that the availability of low molecular weight compounds limits microbial intracellular respiration in our soils, and not the availability of a stoichiometric supply of nutrients, is supported by our results, which reveal greater N mineralisation in soils incubated at 15°C or oscillated between 5°C and 15°C, compared with those incubated at 10°C or 5°C.

Total C generally decreased (Figure 3c) and total N generally increased (Figure 3e) with increasing incubation temperature, resulting in a significantly lower C/N ratio in soils incubated at higher temperatures (Figure 3f), which lends support to our interpretation that, at higher temperatures, readily available C is being depleted and N being mineralised. This evidence, coupled with the lack of leaching or plant uptake allowed in the experiment, suggests that the C left in the soil is more microbially processed (Bach et al., 2018) and more stable. The soluble fractionations of C and N in the soils incubated under oscillating temperature are most similar to the constant 15°C incubation treatment, indicating that changes to C and N are dictated by maximum daily temperature rather than average daily temperature or minimum daily temperature. Soil microorganisms adapt to these changes in C and N availability to fulfil their energy and nutrient demands, thus causing a shift in microbial community composition and physiology (Wan et al., 2014; Schnecker et al., 2015). However, shifts in community composition may also occur due to different groups of organisms outcompeting others for resources at a given temperature (Crowther et al., 2014).

4.4 | Physiological adaptation and acclimatisation of the soil microbial community to temperature regimes

In response to higher temperatures and substrate depletion, microorganisms are able to alter the composition of

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their cell walls to increase membrane stability (acclimatisation), but it is not possible, using fatty acid biomarkers, to distinguish between this phenomenon and a shift in the composition of the microbial community to one that comprises organisms with inherently more stable membranes (Frostegård et al., 2011). Commonly used microbial stress indicators include changes to the ratio of cyclopropyl fatty acids to their cis mono-unsaturated precursors, the ratio of Gram-negative/Gram-positive bacteria, cis/trans ratio, and iso/anteiso branching ratio (Kaur et al., 2005; Feng & Simpson, 2009; Ruess & Chamberlain, 2010; Sizmur et al., 2011; Willers et al. 2015; Bai et al., 2017). In our study, we found that higher incubation temperatures resulted in (i) a lower ratio of Gram-negative/Gram-positive bacteria biomarkers, (ii) a higher ratio of cy17:0c/16:1ω7c, (iii) a higher ratio of cis/trans ratio isomerization and (iv) a higher iso/anteiso branching.

Both Gram-negative/Gram-positive ratio and the ratio of cyclopropyl fatty acids to their cis mono-unsaturated fatty acids precursors (cy17:0c/16:1ω7c in this study) are known indicators of temperature-induced nutrient depletions (Bai et al., 2017). Changes in cis/trans ratio isomerisation and iso/anteiso branching have also been used to explain bacterial physiological adaptations (Ruess & Chamberlain, 2010) under stress conditions. The combination of these indicators could also represent microbial adaptation to sub-optimal temperature regimes (Siliakus et al., 2017). Stress indicators were similar, although slightly lower, in soils oscillated between 5°C and 15°C, compared with soils incubated constantly at 15°C, indicating that the changes to the phospholipid bilayer may be more associated with temperature than substrate depletion. Microbial adaptation, in the form of changing membrane composition, helps the community to combat environmental change (De Maayer et al., 2014; Feng & Simpson, 2009; Siliakus et al., 2017). Significantly lower ratios of cyclopropyl fatty acids to their cis mono-unsaturated fatty acid precursors (cy17:0c/16:1ω7c) and the iso/anteiso ratio in soils incubated under oscillating temperature, compared with those soils incubated constantly at 15°C, reveals that temperature effects on the microbial community are lower in diurnally oscillating soils, compared with soils incubated at constant temperature. This observation could be because the oscillating treatments make the best use of the diversity of the microbial community in the oscillating treatment, since different species may be capable of occupying different "temperature niches" in a fluctuating environment (Upton et al., 1990). Our results thus imply that soil microbial communities incubated in fluctuating environments are less sensitive to temperature change, compared with those incubated under constant conditions (Hawkes & Keitt, 2015).

5 | CONCLUSIONS

We demonstrate that the daily maximum temperature a soil is exposed to has an important impact on soil microbial community composition, soil respiration, and the depletion of soil organic matter in a temperate grassland soil. This is an important observation because asymmetric warming is being observed whereby daily maximum temperatures increase less than daily average or daily minimum temperatures. Soil carbon models that simulate the temperature sensitivity of soil respiration based on laboratory observations made at constant temperatures (e.g., laboratory-derived Q_{10} values) may therefore overestimate the impact of global warming on soil heterotrophic respiration. We propose the inclusion of daily maximum temperature as a parameter in the next generation of soil carbon models.

AUTHOR CONTRIBUTIONS

Adetunji Alex Adekanmbi: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (equal); visualization (equal); writing – original draft (lead); writing – review and editing (supporting). **Xin Shu:** Formal analysis (equal); visualization (supporting); writing – review and editing (supporting). **Yiran Zou:** Formal analysis (supporting); methodology (supporting); project administration (supporting); writing – review and editing (supporting). **Tom Sizmur:** Conceptualization (equal); data curation (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (equal); resources (lead); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (lead).

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DATA AVAILABILITY STATEMENT

Data supporting this publication is available online under a Creative Commons Attribution 4.0 International license at http://dx.doi.org/10.17632/8ng5gf75vw.1

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