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META-ANALYSIS

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The global biogeography of soil priming effect intensity

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Abstract

Aim: Fresh carbon (C) inputs to the soil can have important consequences for the decomposition rates of soil organic matter (priming effect), thereby impacting the delicate global C balance at the soil–atmosphere interface. Yet, the environmental factors that control soil priming effect intensity remain poorly understood at a global scale.

Location: Global.

Time period: 1980–2020.

Major taxa studied: Soil priming effect intensity.

Methods: We conducted a global dataset of CO_2 effluxes in 711 pairwise soils with ^{13}C or ^{14}C simple C sources inputs and without C inputs from incubation experiments in which isotope-labelled C was used to quantify fresh C-induced rather than exudate-induced priming.

Results: Soil priming effect intensity is predominantly positive. Soil texture and C content were identified as the most important factors associated with priming effects, with sandy soils from tropical and mid-latitudes supporting the highest soil priming effect intensity, and soils with greater C content and fine textures from high latitudes maintaining the lowest soil priming effects. The negative association between C content and soil priming effect intensity was also indirectly driven by changing mean

Chengjie Ren and Fei Mo contributed equally to the work.

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annual temperature, net primary productivity, and fungi : bacteria ratio. Using this information, we generated a global map of soil priming effect intensity, and found that the priming was lower at high latitudes and higher at lower latitudes.

Main conclusions: Global patterns of soil priming effect intensity can be predicted using environmental data, with soil texture and C content playing a predominant role in explaining in priming effects. These effects were also indirectly driven by climate, vegetation and soil microbial properties. We present the first global atlas of soil priming effect intensity and advance our knowledge on the potential mechanisms underlying soil priming effect intensity, which are integral to improving the climate change and soil C dynamics components of Earth System models.

KEYWORDS
climate change, global atlas, global drivers, priming effect intensity, soil C dynamics, soil texture

1 | INTRODUCTION

Earth's soils contain more carbon (C) than the vegetation and atmosphere combined and play an important role in regulating ecosystem functions and services such as the modulation of atmospheric CO_2 concentrations, climate change, and biodiversity conservation (Lehmann & Kleber, 2015). Consequently, even a small loss of soil organic C (SOC) can cause a significant increase in the atmospheric CO_2 concentration (Davidson & Janssens, 2006). The soil priming effect, the change in the microbial decomposition of SOC in response to fresh C inputs (i.e., litter input or root exudation of carbohydrates), is a key component of global C cycling (Kuzyakov, 2010; Kuzyakov et al., 2000). Incorporating soil priming effects into earth system models (ESMs) could potentially improve the prediction of global C stocks (Guenet et al., 2018; Sulman et al., 2014). However, the magnitudes of priming effects among various ecosystems remain highly uncertain, with potential soil C release ranging from a 380% increase to a 50% reduction, which greatly impedes the priming representation in ESMs (Guenet et al., 2018; Huo et al., 2017). The uncertainty regarding this soil phenomenon is partly due to the fact that soil C balance is greatly regulated by intricate above- and below-ground interactions (Bastida et al., 2019; Liang et al., 2018). In soil, fresh C inputs contribute to soil C sequestration, but can also alter the decomposition of SOC (Blagodatskaya & Kuzyakov, 2008; Kuzyakov et al., 2000). Therefore, knowledge of the global biogeographical distributions of soil priming effects is crucial for accurately predicting soil C dynamics under climate change.

Geographical distributions of soil priming effects are driven by both abiotic and biotic factors (Bastida et al., 2019; Guenet et al., 2018; Liang et al., 2018). Previous studies have identified climate factors (temperature and moisture; Reinsch et al., 2013), plant properties (i.e., litter quality and quantity; Fanin et al., 2020; Pascault et al., 2013), soil properties (SOC content and stability, pH; Bastida et al., 2019; Chen et al., 2018, 2019), and microbial attributes (microbial biomass, diversity, and community structure; Fontaine et al., 2003; Liang et al., 2018; Razanamalala et al., 2018) as potential drivers of soil priming effects. Despite these findings providing useful information on the environmental drivers of soil priming effects across local and regional-biome, a systematic and holistic understanding of soil biogeography of priming effects and their dominant drivers is lacking at the global scale (Guenet et al., 2018; He & Xu, 2021; Wieder et al., 2013). Moreover, it is widely accepted that the direction and intensity of soil priming effects are regulated by a succession of processes rather than singular mechanisms (Kuzyakov et al., 2000), the fresh C input-induced soil priming effect is a general phenomenon that occurs in various terrestrial ecosystems involving diverse substrates, but we are still lacking a simple and generalizable framework to explain this important soil process (Liu et al., 2020). As such, the assessment of global soil priming effects should consider both abiotic and biotic factors simultaneously. Quantitative understanding of the global drivers of soil priming effect intensity can help to quantify the contributions of priming to climate warming feedbacks and increase the accuracy of ESMs.

To address these knowledge gaps in biogeographical patterns for soil priming effect intensity, we conducted a global synthesis of CO_2 effluxes in 711 pairwise soils with ^{13}C or ^{14}C labelled simple C sources inputs (e.g., glucose, organic acids, lignin, and cellulose, etc.) and without C inputs from incubation experiments (Figure 1, Supporting Information Table S1). Based on these incubation experiments, a one-pool biogeochemical model was used to model soil C decomposition (see Methods). We then calculated the priming effect intensity and further analysed its macroscopic properties to develop an empirical model for it. Finally, we mapped soil priming effect intensity globally. In this study, we aimed to (a) explore the global drivers of soil priming effect intensity, and (b) investigate the biogeography of soil priming effects and create the first global atlas of their intensity.

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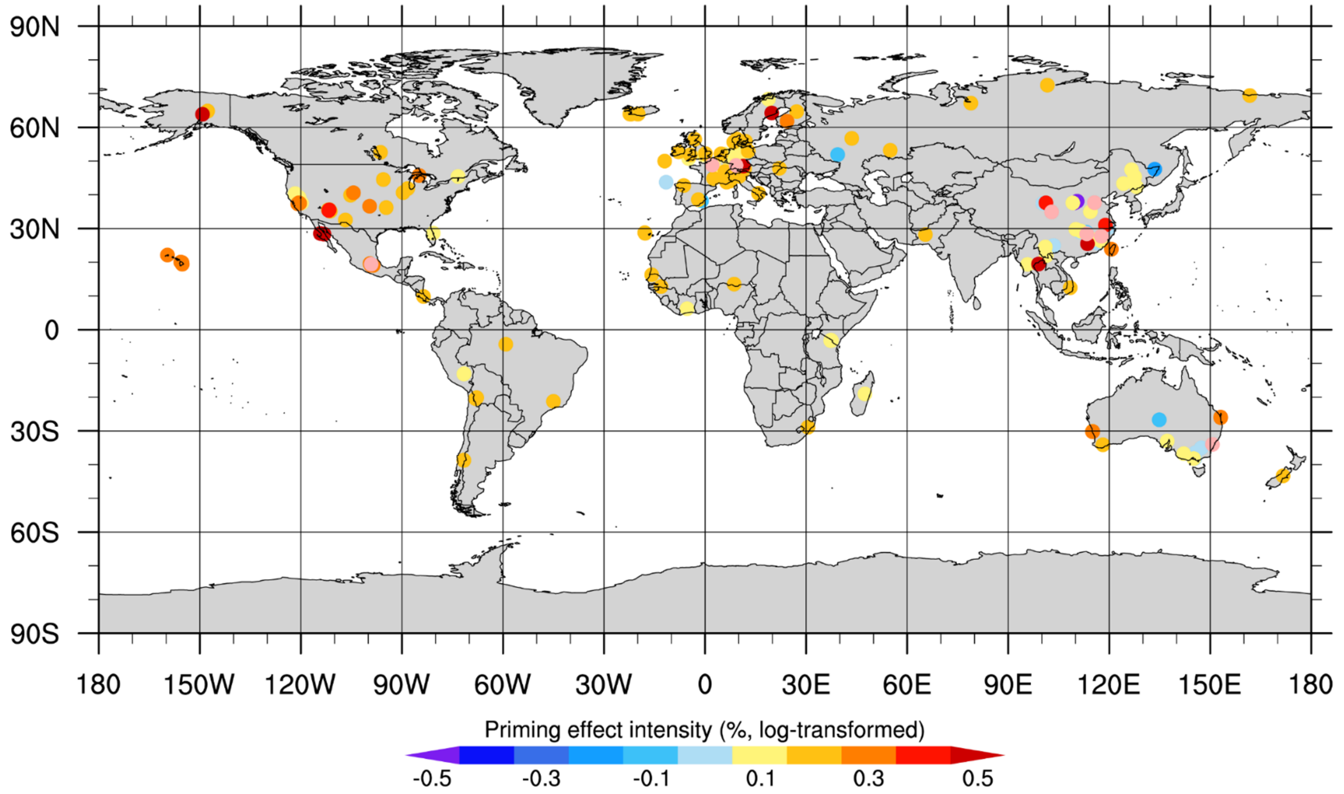

FIGURE 1 Spatial distribution of the data points used in this study

2 | METHODS

2.1 | Data sources and preparation

The ^{13}C or ^{14}C labelled fresh C addition experiment is a common approach for quantifying the priming effects of SOC, which is traditionally expressed as a percent increase in CO_2 emission from the old C under the new C addition treatment relative to that in the control. Thus, soil priming effects are calculated as the difference between the soil respiration derived from old C after fresh C input and that derived from the control samples. In order to investigate the global patterns of priming effects, a comprehensive literature survey was conducted through Google scholar (http://scholar.google.com/) from 1980 to 2019; the keywords were 'soil' and 'incubation' and 'isotope' and 'carbon.' Articles were selected based on the following criteria: (a) both control and isotope-labelled simple C addition (e.g., glucose, organic acids, lignin, and cellulose, etc.) treatments were included in the same incubation experiments; (b) at least three time-course measurements of CO_2 emission rates were reported under control and isotope-labelled simple C addition treatments, and these CO_2 emission rates could be partitioned into native C-derived CO_2-C (^{12}C) and simple C-derived CO_2-C (^{13}C or ^{14}C) based on the isotopic signature of CO_2-C; (c) all the incubation soils were from the topsoil (~20 cm); (d) the initial soil C and the amounts of added fresh C had to be available; and (e) if different publications included the same data from one study, we recorded the data only once. Finally, a total of 711 paired experiments (treatment versus control) were included in the present study (dataset). For each paired experiment, we extracted the observed C mineralization data including treatment-induced cumulative total CO_2, fresh C- and native SOC-derived CO_2, as well as the cumulative total CO_2 from the control at each time point of the time-course measurements.

Furthermore, we extracted the data relevant for the site background, edaphic, microbial, and incubation information for these 711 paired experiments. These variables included latitude, longitude, climatic factors, bulk density (BD), soil pH, soil texture (sand, silt, and clay fraction), soil organic C content (SOC), total nitrogen (TN), C : N ratio, soil microbial properties, and the amount of fresh C addition. However, if the environmental variables were not fully reported in a published study, we extracted the required data from global datasets based on the latitude and longitude (Supporting Information Table S2). Specifically, for climatic factors, we extracted mean annual temperature (MAT) and mean annual precipitation (MAP) during 2006–2015 from global atmospheric re-analysis II data of the National Centers for Environmental Prediction (NCEP-2). In addition, vegetation properties (gross primary production, GPP; net primary productivity, NPP) for the period 2006–2015 were obtained from the moderate resolution imaging spectroradiometer (MODIS) products (MOD17A3) (Yuan et al., 2020). We also obtained data for soil pH, BD, soil texture (i.e., sand, silt, and clay), and soil substrates (SOC, TN, C : N) from version 1.2 of Harmonized World Soil Data (https://daac.ornl.gov/SOILS/guides/HWSD.html). Soil microbial properties (fungal biomass C, bacterial biomass C, and fungi : bacteria ratio) were also retrieved from a global fungal and bacterial biomass C dataset compiled by He et al. (2020) (Supporting Information Table S2).

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2.2 | Calculation of modelled priming effect intensity

A one-pool biogeochemical model was used to model soil C decomposition (van Groenigen et al., 2014) using the incubation datasets with a Bayesian Markov chain Monte Carlo method (Hararuk et al., 2014). The model validation confirmed the robustness of our empirical model for global priming effects (Figure 2); order equations are shown below:

$$\frac{dN^1}{dt} = N^1 - K_N \times N^1 \tag{1}$$

$$\frac{dC^1}{dt} = K_N \times N^1 \times r - K_{O_c} \times O_c^1 \tag{2}$$

$$\frac{dN^n}{dt} = -K_N \times N^n \tag{3}$$

$$\frac{dC^n}{dt} = K_N \times N^n \times r - K_{O_c} \times O_c^n \tag{4}$$

$$\frac{dC}{dt} = -K_{O_t} \times O_t \tag{5}$$

where N^1 is the fresh-C input rate (mg C/g soil/day), which is the amount of added substrate C in the isotope-labelled C addition treatment at time 0, N^n is the size of the N pool after a period (n) of decomposition. There is no N pool for the control (i.e., no C addition). O_c^1 and O_c^n are the pool of native C at time 0 and time n in treatment. O_t is the pool of native C in the control. K_N, K_{O_t}, and K_{O_c} are decay rates of the N pool, and of the native C pool in the treatment and control, respectively. r is the transfer coefficient (unitless) from the newly added fresh C to soil C pool. The priming effect intensity was calculated as shown below:

$$\text{Priming effect intensity}\,(\%) = \frac{(K_{ot} - K_{oc})}{K_{oc}} \times 100 \tag{6}$$

2.3 | Potential predictors for priming effect intensity

Structural equation modelling (SEM) was used to graphically show the influence of each variable in the model, when the other variables in the model were held statistically constant. Before SEM, the Moran's I test statistic for spatial correlation (Moran, 1950) was calculated to reduce the random effects from the location. The value of Moran's I was .454 and the p value = .073 > .05, which indicated that priming effect intensity among our sample sites had no spatial autocorrelation. Thus, when designing the SEM, the space effect was not considered; however, other environmental variables including climate factors (MAT, MAP), vegetation properties (GPP, NPP), soil properties (bulk density, silt, clay, pH, SOC content, total nitrogen), and microbial properties (fungal biomass C, bacterial biomass C, and

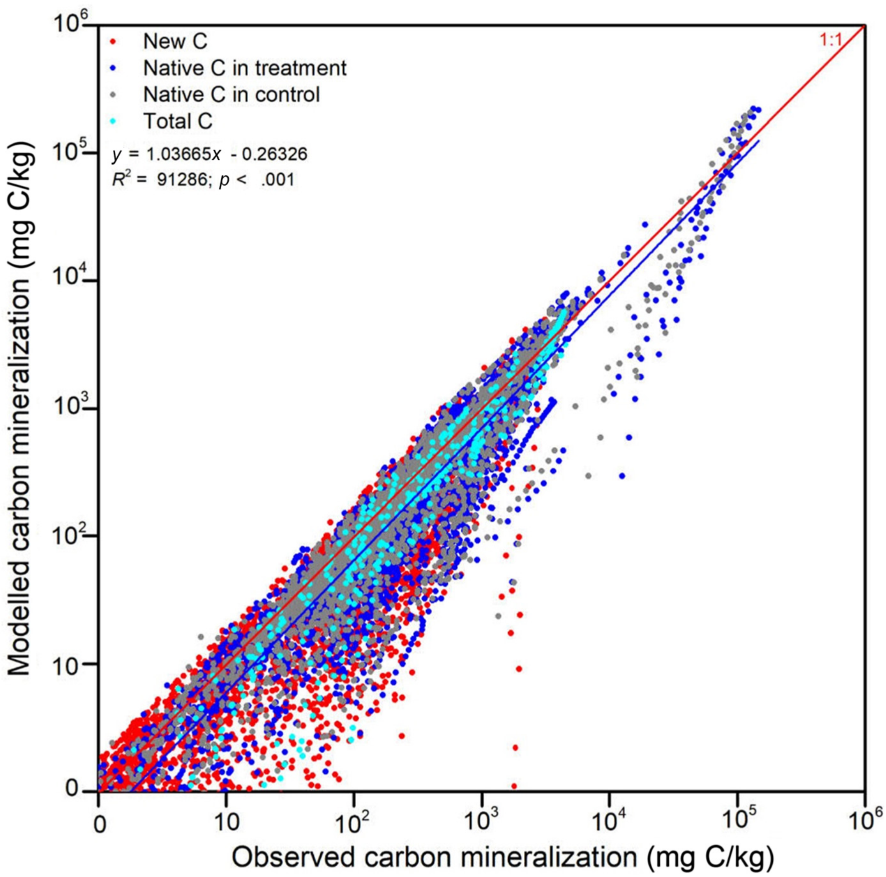

FIGURE 2 Observation versus simulation values of priming effect intensity (%). The 1:1 dotted line is plotted

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the ratio of fungi to bacteria biomass C (F : B ratio)] were considered. Moreover, two types of statistical models (random forest analysis and generalized linear model) were used to test the relative importance of predictor variability for priming effect intensity. First, the visualizations of random forests were chosen to show the partial feature contributions of the most important variables (Supporting Information Figure S2). The plots were arranged according to variable importance, and the goodness-of-visualization was evaluated with leave-one-out *k*-nearest neighbour estimation (R^2 values). For example, for the microbial properties' groups, the R^2 for the F : B ratio was significantly higher than those for both fungal biomass carbon and fungal biomass carbon; thus, the F : B ratio was more important than these other two factors. Second, the generalized linear model was also used to show the important factors for changed priming effects. Generally, if the important value was higher (shown on the horizontal axis), the variable was considered as the predominant factor (Supporting Information Figure S3). After attaining a satisfactory variables, we introduced composite variables into our model. The use of composite variables did not alter the underlying SEM model, but collapsed the effects of multiple conceptually related variables into a single composite effect, aiding interpretation of model results. Also, before SEM analysis, an a priori model was built to explore the direct and indirect effects (Supporting Information Figure S4). All the analyses were conducted using the R statistical software environment v.4.0.2 (https://www.r-project.org/).

2.4 | The empirical model for global priming effect intensity

An empirical model was developed to estimate the priming effects with consideration of the primary controlling factors from the SEM analysis. The log-transformation was used to a normal distribution for robust statistical analysis. Two-thirds of the observed data points were used to build the model, while the one-third of the data points were used to evaluate the model (Supporting Information Figure S5). We then built the model based on the 14th degree polynomial regression function before Akaike information criterion (AIC) selection. The full primary model is shown below:

$$\begin{aligned} PE = &\ a1MAT + a2MAT + a3GPP + a4NPP + a5SOC + a6TN \\ &+ a7C{:}N + a8pH + a9Silt + a10S\,and + a11Clay \\ &+ a12FBC + a13BBC + a14F{:}B + b \end{aligned} \tag{7}$$

where a1–a14 are the coefficients for the primary corresponding controlling factors and b is the primary intercept. After choosing by the lowest AIC score, the final empirical model for predicting priming effects is shown below:

$$PE = a1'MAT + a2'NPP + a3'SOC + a4'pH + a5'Ssilt + a6'Sand + a7'F{:}B + b \tag{8}$$

where a1'–a7' are the coefficients for the corresponding controlling factors and b is the intercept (Supporting Information Table S3). Based on the global biome classification criteria, we summarized the differences in priming effects across 12 major terrestrial biomes: boreal forest, temperate coniferous forest, temperate broadleaf forest, tropical forest, mixed forest, grassland, shrubland, tundra, desert, natural wetlands, cropland, and pasture. Most statistical analyses were conducted using the free software environment R (https://www.r-project.org/). Resample processes were carried out and the global maps created using NCL (National Center for Atmospheric Research Command Language, version 6.5.0, https://www.ncl.ucar.edu/).

3 | RESULTS AND DISCUSSION

3.1 | Global drivers of soil priming effect intensity

We found that soil priming effect is a global phenomenon (Guenet et al., 2018), with positive soil priming effect observed in 560 soils (79%) and a negative soil priming effect observed in 151 soils (21%) (Figure 1, Supporting Information Figure S1). SEM was conducted to identify the most important environmental factors associated with soil priming, and found that soil texture and SOC content are the fundamental drivers of soil priming effect intensity globally (Figure 3). Highly positive soil priming effect intensities are more likely to be observed in sandy soils (Bastida et al., 2019; Fontaine et al., 2004). In these soils, typically found in deserts and tropical regions, microbial communities are known to be adapted to the rapid recycling of organic matter, which promotes high C mineralization rates, when mining for other nutrients (Bastida et al., 2019). Higher soil priming effects are associated with greater sand content globally (Figure 3), suggesting that soil priming effects are greater in coarser soils. Sandy soils are often associated with low C contents (Delgado-Baquerizo et al., 2020), and could support positive soil priming effect intensity in response to fresh C inputs. On the contrary, soils with higher silt content are associated with a negative soil priming effect (Figure 3). First, fine mineral particles contribute to the formation of microaggregates, which limit microbial access to SOC due to spatial inaccessibility (Chen et al., 2019). Second, fine soils contribute to the stabilization of SOC by mineral protection, that is, interactions between SOC and fine mineral particles due to ligand exchange, polyvalent cation bridges, and complexation (von Lutzow et al., 2006). Further, our findings show that SOC is a direct driver for changed priming effect intensity, and had significantly negative associations globally, indicating that the initial C content regulates the directions and magnitudes of priming effect intensity (Figure 3). Importantly, soils with greater C content, such as those found in high latitudinal ecosystems in the Northern Hemisphere, are expected to have negative soil priming effect intensity (Figure 3). A possible reason for this is that, under high C conditions, fresh C is invested by microbes in producing newer biomass as well as using the C accumulated in organic matter, resulting in negative priming effects. In line with our results, negative relationships between soil priming effect intensity and SOC content have been widely reported by previous

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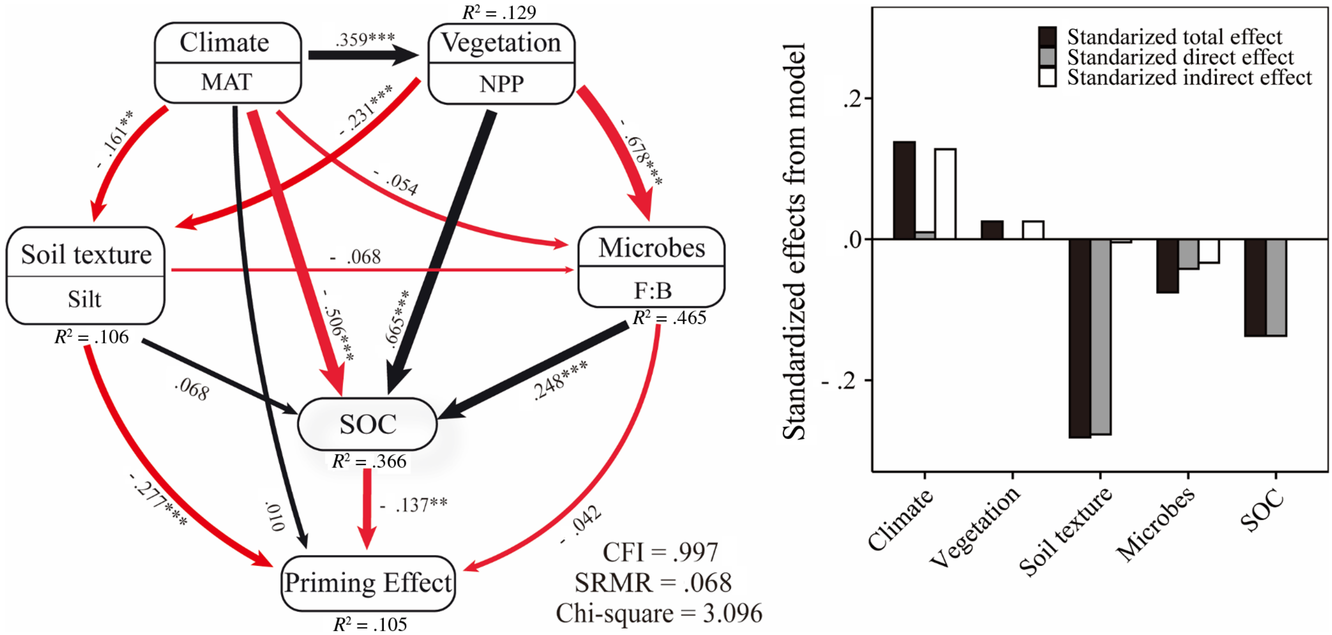

FIGURE 3 Direct and indirect effects of climate, vegetation, and soil and microbial properties on the priming effect. The arrows indicate the hypothesized direction of causation. Black and red arrows indicate positive and negative relationships, respectively. The arrow width is proportional to the strength of the relationship. MAT = mean annual temperature; NPP = net primary productivity; SOC = soil organic carbon; F : B = the ratio of fungi to bacteria biomass C. The numbers adjacent to the arrows are the standardized path coefficients. An a priori model associated with this figure is available in Supporting Information Figure S4. Significance is represented by *** $p < .001$, ** $p < 0.05$

local and regional studies (Bastida et al., 2019; Chen et al., 2014; Guenet et al., 2018).

In addition, the results of SEM analysis revealed the indirect association between ecological predictors and soil priming effect intensity (Figure 3). For example, the negative association between C content and soil priming effect intensity was found to be indirectly driven by climate, which is not unexpected as colder and more productive soils often support higher C contents (Guenet et al., 2018). Soils from warmer climates are known to accumulate less C as a consequence of the higher C decomposition and respiration rate (Thiessen et al., 2013; Yuste et al., 2007). Similarly, NPP can also control the chemistry of plant litter and root exudates, which can increase microbial metabolism (Waldo et al., 2019; Zhang et al., 2017) and shape microbial community composition (direct effect: $r = -.678$), thereby affecting the C dynamics and indirectly driving soil priming effect intensity globally. Previous observations have also shown the association between soil priming effects and the quantity and quality of plant C inputs over broad geographical scales (Huo et al., 2017; Luo et al., 2015), supporting this idea. Notably, our results also showed that soil F : B ratio had no direct effect on priming effect intensity but indirectly drove it through modification of SOC (Figure 3), implying that the magnitudes of priming effect intensity were mainly determined by the different microbial groups mediating C dynamics (Blagodatskaya & Kuzyakov, 2008; Davidson & Janssens, 2006). Specifically, fungi have generally more oligotrophic features and can produce a wide range of enzymes that allow the degradation of recalcitrant fractions (Eichlerova et al., 2015; van den Brink & de Vries, 2011). Bacteria show a wide metabolic diversity and often an opportunistic strategy that allow them to rapidly absorb labile substrates (Di Lonardo et al., 2017). As such, it may be speculated that the positive association is due to the higher F : B ratio inducing a higher degree of recalcitrant carbon degradation and the priming of SOC. Collectively, these results suggest that changing climate, vegetation characteristics, and microbial properties can indirectly alter soil priming effect intensity by changing soil C content.

3.2 | A global atlas of soil priming effect intensity

Using the most important predictors from the SEM analysis, we extrapolated this relationship to the global scale and generated a global map of soil priming effect intensity. The results revealed a distinct pattern of changes in soil priming effects with latitude (Figure 4 and Supporting Information Figure S6), such that priming was lower at high latitudes (North America and northern Russia) and higher at lower latitudes (i.e., Indonesia, South Africa, and South America). Tundra and boreal forest showed the lowest soil priming effect intensity and subtropical forests showed the highest, predicting that priming-induced C decomposition was higher in warmer regions than that in cold regions. The reason might be associated with the fact that high-latitude colder ecosystems in the Northern Hemisphere often accumulate more C in their soils, compared with

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tropical and subtropical soils. Furthermore, we found higher values of soil priming effect intensity in deserts (Supporting Information Table S1), with relatively low plant productivity but higher temperatures. The positive priming effects in desert areas may be related to the high impact of fresh C inputs on soil microbial communities, which are naturally adapted to low SOC content but often support rapid C cycling (Bastida et al., 2013). The Tibet Plateau, the largest alpine permafrost region in the Northern Hemisphere, showed low soil priming effect intensity, attributable to the large quantities of SOC (Ding et al., 2016) and low temperature. The global atlas also indicates that soil priming effect intensity ranked as tropical forest/subtropical forest > temperate forest.

In summary, this study represents the most comprehensive attempt to date to understand the global patterns of soil priming effect intensity, producing a global map of soil priming effect intensity, and highlighting that priming induces stronger C–climate feedback. Our global atlas of soil priming effect intensity is important to understand where and why C priming could be fundamental to understanding climate change–C feedbacks globally. Soils that are subject to losses in C content associated with natural retrogression (e.g., very old tropical soils), anthropogenic desertification, acidification and agricultural processes might further support higher priming effects in response to fresh C input. Our results suggest that protecting soils in boreal and cold regions wherein C is accumulated is now more important than ever before. Previous earth system models did not include priming mechanisms and spatial heterogeneity in the global C models (Blagodatskaya & Kuzyakov, 2008); however, our results suggest that they are fundamental to properly incorporate the impacts of soil environments into the capacity of soil to capture C. Thus, in future work, including soil priming effects in earth system models should be considered to allow for accurate assessment of global soil C stocks.

3.3 | Limitation and uncertainties

In this section, we acknowledge some limitations of our study. First, the distributions of observed data were disproportionate among different regions, which may have caused biases when establishing the global empirical priming effect model. Second, the environmental variables were not fully reported in each case and the data extracted from global datasets are likely to have added uncertainty to the analyses. In addition, the modelling uncertain from the driving datasets must be considered when we generated the global map of soil priming effect intensity. In spite of these limitations, our study constitutes the biggest effort to understand the drivers of soil priming effect intensity at the global scale. Future priming studies and observational studies should be changed to a wide range of scales to clarify the underlying patterns and controls of priming effect intensity.

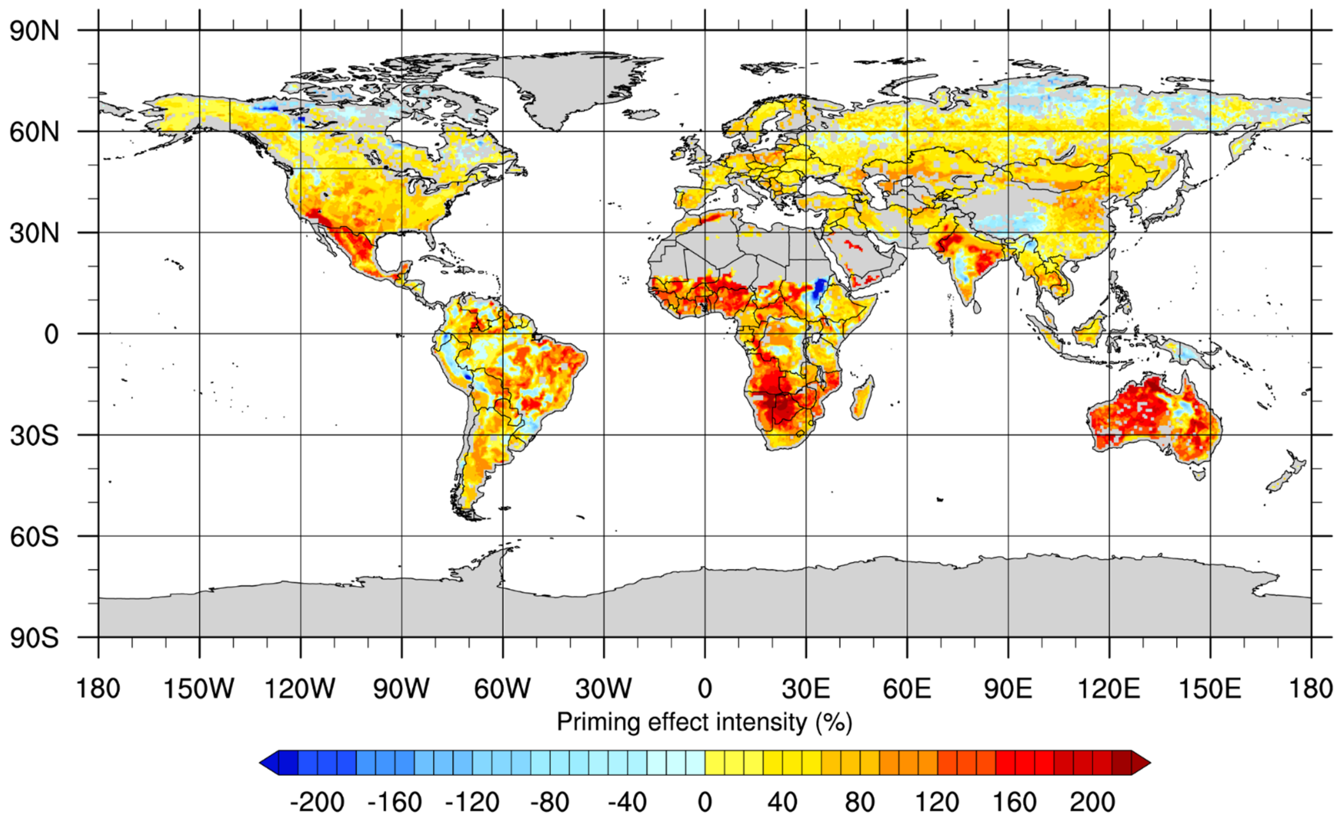

FIGURE 4 Global pattern of priming effect intensity (%)

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AUTHOR CONTRIBUTIONS

C.R. and G.Y. conceived the project. C.R., Y.L., T.J.G., G.W., G.R., X.W., K.Y. and J.W. contributed ideas to the analysis. X.Z., Z.Z., Z.Z. and X.Z. compiled the database. C.R., F.M. and G.Y. analysed the data. C.R., Z.Z., F.B., M.D.B. and Z.Z. wrote and revised the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are uploaded in figshare at https://doi.org/10.6084/m9.figshare.17451893.v1.

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