Global ecological predictors of the soil priming effect

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Soil priming, the change in the microbial decomposition of soil organic carbon (SOC) in response to fresh carbon (C) inputs, is expected to influence C cycling globally. However, the global ecological predictors of priming remain elusive. Soil priming has two components: apparent priming, which is due to microbial biomass turnover, and real priming, which corresponds to the change in soil organic matter mineralization. Here, we conducted a global survey of soils from 86 locations, spanning six continents and a wide range of climates, vegetation, microbial community composition, and soil conditions, and evaluated the apparent soil priming effect using ^{13}C-glucose labeling for 16 days under potential conditions of temperature and water content. The magnitude of the positive apparent priming effect (increase in CO_2 release through the accelerated microbial biomass turnover) was negatively associated with SOC content and microbial respiration rates. Our statistical modeling explained ~80% of the global variation in apparent soil priming and suggested that, in more mesic sites associated with higher SOC contents, apparent soil priming effects are more likely to be negative. In contrast, a single-input of labile C caused positive apparent priming effects in more arid locations, associated with low SOC contents. Our results suggest that the SOC content plays critical role in regulating apparent priming effects globally, with important implications for the prediction of priming-derived C fluxes under global change scenarios and for the improvement of global C cycling models.

Soil contains more C than the atmosphere and aboveground plant biomass combined (the top three metres of soil stores more than 2300 Pg C) [1,2]. Carbon dioxide (CO_2) efflux from soils is one of Earth's largest fluxes of C to the atmosphere[1]. An important part of such efflux can result from the turnover of the soil microbial biomass, which is sensitive to environmental changes[3,4] and is estimated to contain up to 23.2 Pg C within the first top 100 cm of soil[2]. Soil priming, the change in the microbial decomposition of soil organic carbon (SOC) in response to fresh carbon (C) inputs, is a key component of global carbon C cycling[5-7]. Priming is divided in two components: apparent priming corresponds to change in the CO_2 evolved from microbial biomass turnover after the input of easy-available substrates, and the real priming effect which corresponds to the change in the CO_2 release from soil organic matter [7,8]. These two components of priming are difficult to distinguish, however, apparent priming tends to occur shortly after adding readily availably substrates (first days and weeks), while real priming takes longer [7,9].

Overall, soil priming is a complex phenomenon that is regulated by multiple mechanisms, involving abiotic and biotic factors (including, but not limited to, nutrient availability, catabolism of different organic matter pools)[6,7,10,11]. Soil priming has been postulated to be a major determinant of the capacity of soils to function as sources or sinks of atmospheric CO_2[12]. Consequently, inputs of fresh organic matter to the soil can cause an accelerated microbial biomass turnover (apparent priming). Alternatively, a negative priming due to reduced SOC mineralization or attenuated microbial biomass turnover can occur when labile C is added to soil[6]. Recent modelling developments suggest that soil priming is a strong candidate for inclusion in models to predict global distributions of C because of the important role of priming in determining the exchange of C between soils and the atmosphere [5,13]. However, we lack a unifying ecological context and an integrative approach to understanding soil priming effects globally, which would allow us to determine how the direction of the priming effect varies across different ecosystems and why this variation exists.

A growing body of literature has identified nutrient availability, climate, soil type, or plant and microbial attributes[14-18] as potentially important drivers of priming[7]. For example, soil texture has been demonstrated to be an important factor controlling the soil priming effect, and plants, through the amount and composition of rhizodeposits, also play a key role in mediating priming effects[4]. Furthermore, climatic factors such as mean annual temperature are related to soil priming effects[11]. However, in spite of the elevated amount of C within microbial biomass[2], a comprehensive understanding of the drivers of the apparent priming effect across major biomes and gradients at the global scale is lacking. This knowledge will shed light on how environmental factors regulate the microbial biomass turnover and its contribution to CO_2 fluxes under global change scenarios[19,20]. Moreover, a better understanding of the ecological predictors of priming will improve our ability to predict how CO_2 fluxes might shift in response to human and global change factors that influence the quality and quantity of fresh C inputs to soil and soil microbial responses[12], such as afforestation[21], changes in plant C allocation to soil due to the elevated levels of atmospheric CO_2[12], the addition of organic amendments to soil[22], nitrogen (N) deposition[23], warming[24] and changes in land use[25].

Herein, we conducted a soil survey of 86 locations across six continents, spanning multiple climates (tropical, temperate, polar, arid and continental) and ecosystem types (e.g., forest, grasslands and croplands; SI Appendix, Fig. S1). We aimed to identify the major global ecological predictors of the apparent soil priming effect. Apparent priming was determined using a soil incubation of 16 days coupled with ^{13}C-labeled glucose. Ecological predictors included wide environmental gradients of mean annual temperature, aridity, vegetation types, plant cover, soil chemical and physical properties, and microbial attributes (microbial respiration, biomass and original soil community composition of bacteria and fungi). Moreover, information on the microbial populations potentially associated with the apparent priming effects remains limited[18]. Therefore, considering microbial attributes, as we have done here, is critical in evaluating the environmental factors predicting the apparent priming effect.

Given that SOC is widely correlated with microbial biomass[26], we hypothesized that the effect size and the direction of the apparent priming effect is regulated by SOC content, which, in turn, is modulated by the environmental and ecological context of each soil[27,28]. Thus, we hypothesized that soils with lower SOC content, including soils from arid sites with sparse plant cover where microbial biomass is strongly limited by C[29], will be more responsive to the inputs of labile C, ultimately stimulating microbial turnover and the resulting apparent priming-mediated CO_2 release (positive priming)[7]. Conversely, we expected that the apparent priming effect would be negative in soils from mesic regions with greater plant cover and higher litter and root inputs to soil where microbial biomass and soil microbial respiration are less limited by the availability of C.

Results and Discussion

Considering that incubation with ^{13}C-glucose lasted 16 days, our results mainly reflect the patterns of the apparent priming effect[7,8]. It corresponds to changes in CO_2 release as a consequence of microbial biomass turnover shortly after adding fresh-available substrates[7,8]. Our findings indicate that the apparent soil priming effect is a globally ubiquitous phenomenon and provide new insight into its major ecological predictors, in spite the extreme heterogeneity of soils and incubation limitations, as described below.

We found contrasting responses of apparent priming associated with different globally distributed ecosystem types. In some soils, a single-pulse of labile C accelerated the

turnover of microbial biomass (positive apparent priming). Conversely, the addition of labile C can lead to reductions in microbial turnover in other soils (negative apparent priming; Fig. 1A-B). For instance, positive apparent priming effects were associated with shrub- and forb-dominated ecosystems, croplands and cold forests (Fig. 1A). In some ecosystems (i.e. croplands, forblands and shrublands), the release of CO_2 due to positive apparent priming represented more than 20% of the basal microbial respiration rate (Figs. 1C-D). Nevertheless, the magnitude of the positive apparent priming effect was low as a fraction of the total SOC pool (with a maximum of the 0.13% of the SOC being mineralized due to priming in cold forests; SI Appendix, Fig. S3) which likely corresponds to the CO_2 released by acceleration of microbial turnover. As mentioned previously, the aim of this study was not to determine the absolute values of priming effects *per se*, but we would have expected even greater priming responses in a longer incubation experiment[9], that would probably account for real priming effects, or under field conditions. In contrast, we found negative apparent priming effects in grasslands, and particularly, in soils with very high SOC contents (e.g., volcanic soils from Hawaii) (Dataset, Supporting Information). These findings suggest that apparent priming responses are ecosystem dependent. In other words, the importance of the apparent priming-derived CO_2 in soils with the highest organic C content, such as those in tropical ecosystems[30], is typically lower than in other ecosystems supporting lower levels of soil C such as drylands and croplands[31] (Fig. 1C-D).

Our work is consistent with the results of previous studies showing that priming occurs in most soils[14,17,18]. Previous studies have demonstrated that priming is modulated by plants and rhizodeposits[17], microbial diversity[18] and warming[24]. Here, we decipher the ecological context that regulates the apparent priming effect by considering a large range of soils that varied in their abiotic and biotic factors. Our study suggests that a single pulse of labile C can cause contrasting responses of apparent priming (microbial turnover) across a wide gradient of soil and ecosystem types. These results have implications for the prediction of C fluxes under forecasted global change and for the improvement of global C cycling models. Nevertheless, we acknowledge some limitations of our study. First, the size of the incubation (1 g of soil) did not sufficiently account for the presence of macroaggregates. However, it is known that soil aggregates are critical for C sequestration[32,33] and that aggregate disruption through sieving can influence priming effect patterns[34]. Given their connection with C sequestration, further models of priming should also consider the content of aggregates. Second, incubation conditions in our study differed from those likely experienced in the field (i.e. different temperature and soil water content). Consequently, our results should be interpreted as potential patterns of apparent priming. Even if our experimental incubation does not fully replicate *in situ* conditions, such experimental data can be used to evaluate assumptions underlying microbially-explicit soil biogeochemical models, and help to identify how microbial processes and edaphic factors can drive apparent priming at the global scale.

Here, we used structural equation modeling (SEM; *a priori* model in SI Appendix, Fig. S4) to provide integrative information on the major ecological predictors of apparent soil priming across a broad range of soil types from different ecosystems and climates (SI Appendix, Fig. S1; see Material & Methods). SEM is particularly useful in large-scale studies, as it allows us to partition causal influences among multiple variables, and to separate the direct and indirect effects of the predictors included in the model[35]. Further, SEM is capable of accounting for continuous and categorical variables. Our model included important geographical and ecological factors such as climate (aridity [ARI], calculated as 1- the Aridity Index, which is negatively related to mean annual

precipitation and mean annual temperature [MAT]), variables related to soil C (basal microbial respiration rates and total organic C), soil properties (Olsen phosphorus [soil P], pH, clay + silt and salinity), plant cover, dominant vegetation type (forests, shrublands, grasslands and croplands), and important microbial features such as microbial biomass (*via* substrate-induced respiration [SIR]), and the relative abundance of selected microbial taxa from the original microbial community in our soils (see Methods). Before conducting our SEM, we checked for potential multicollinearity among the selected ecological predictors. None of the predictors included in our SEM suffer from multicollinearity ($r < 0.8$), and therefore, multicollinearity issues wee not expected in this model. Note that our SEM did not examine an explicit direct effect of aridity and mean annual temperature (MAT) on either apparent priming or respiration rates (as soils were incubated under controlled laboratory conditions). However, we included these climatic factors in our SEM to evaluate the indirect effects of climate on apparent priming *via* changes in SOC and plant cover, which we measured under field conditions, therefore providing an ecological context to our results.

In spite of the difficulties for predicting the soil priming effect at the global scale, our SEM approach explained a large portion of the variation in the apparent priming effect worldwide (~80%; Fig. 2), and provided strong evidence that SOC content (ranging from 0.1 to 38%) and basal microbial respiration were directly and negatively associated with apparent priming effects (Figs. 2-4). Importantly, our model goodness-of-fit was strong, indicating that it represents a causal scenario consistent with the data. Strikingly, soil microbial biomass (estimated using substrate-induced respiration, SIR), which has been postulated to be a major ecological predictor of priming effects[7], was not a significant predictor of apparent priming in the wide variety of soils tested here (Fig. 2). In other words, our results suggest that the initial content of SOC ultimately regulates the apparent soil priming effect. Soils with greater C content (therefore, less limited by C) are more likely to exhibit negative or minimal apparent priming. Importantly, the negative relationships between SOC content and apparent priming (Fig. 3A), and between basal respiration and apparent priming (Fig. 3B) were maintained even after tropical soils (the soils with the highest SOC content) were removed (SOC content *vs* apparent priming without tropical soils: $r = -0.27$; $p = 0.015$; basal respiration *vs* apparent priming: $r = -0.67$; $p < 0.001$).

By using amplicon sequencing approaches, we could further investigate associations between soil microbial community composition and the direction of the apparent soil priming effect. We found that soils having higher relative abundance of *Basidiomycota* and *Armatimonadetes* had higher positive apparent priming effects. Conversely, soils with higher relative abundances of *Verrucomicrobia* and *Chytridiomycota* tended to have lower or negative apparent priming effects (Fig. 3; SI Appendix, Table S1). However, in our SEM, only the relative abundance of *Basidiomycota* had significant direct effects on the apparent priming effect after considering multiple environmental factors simultaneously (Fig. 2-4). *Basidiomycota* are dominant and widely-distributed fungi[36] that play important roles as decomposers of plant-derived organic matter [37]. Further, *Basidiomycota* have been reported to become active through the utilization of glucose and to then change their substrate preference to native SOC compounds, which also include microbial necromass as a fundamental component[38,39], once glucose or other labile C compounds are depleted[11]. This mechanism might support the positive apparent priming effects reported here. Further, we highlight the fact that soil was sieved through 2 mm prior to incubation (see Material & Methods) and it might be possible that *Basidiomycota* hyphae were fragmented,

although their DNA can be still present in soil as relic DNA[40]. The subsequent microbial decomposition of fungal hyphae fragments during the incubation could contribute to the apparent positive priming in soils with greater abundance of *Basidiomycota*. Moreover, Basidiomycotal spores and fragments of hyphae (diameter of 4-6 μm vs. sieving at 2000 μm) can resist sieving and develop during the incubation, contributing to the observed priming results. We found 1118 phylotypes classified as *Basidiomycota* in our globally distributed soils. Among these taxa, we selected the most common (present in >10% of all locations) and conducted Random Forest analyses (as described in Delgado-Baquerizo et al. 2016[41]) to identify the most important *Basidiomycota* taxa associated with the magnitude of the apparent priming effect across biomes. We found that taxa associated to apparent positive priming effects belonged to unidentified Agaricomycetes phylotypes (Fig. S5).

Previous studies have suggested that the total content of N and phosphorus (P), as well as C:N and N:P ratios of the soil organic matter (SOM), play a major role in the direction of priming[18]. For instance, Chen et al. 2014[42] found that the interactions between C and N availability influenced the extent of the priming effects. Moreover, other authors have found that priming can be more significant in N- and P-limited soils because microbes need to mine the SOM for such elements in nutrient poor environments[9,16,43]. In contrast, recently novel dual isotope approaches (^{13}C- and P-^{18}O tracers) have revealed a stronger priming effect in soils with larger P contents than in soils with smaller P contents[44]. In our study, which centered on apparent priming effect, soil N content was highly correlated with SOC content ($r = 0.88$; $p < 0.001$), and was therefore not included in our statistical modeling to avoid multicollinearity. Further, available soil P (Olsen P) content did not correlate significantly with the apparent priming effect ($r = -0.27$; $p = 0.81$). In this respect, our study suggests that, across broad gradients in soil P availability, available soil P might have a relatively small role in driving the microbial turnover responsible on the apparent priming effects. Moreover, soil elemental stoichiometry, not included in our *a priori* model, was not correlated with the apparent priming (total N: available soil P: $r = -0.07$; $p = 0.533$ and total organic C: total N: $r = -0.15$; $p = 0.181$). Similarly, physical factors such as soil texture, which has also been proposed as a factor regulating soil priming effects[45], was not a significant factor across the broad range of soils tested here. Other soil properties such as pH, available soil P content and salinity did not show any direct effect on the apparent soil priming, but these factors indirectly affected soil microbes (Fig. 2), and salinity had a total negative significant effect on priming[46,47].

Our SEM provides an ecological context for apparent priming effects across a wide range of soils. Soils with greater plant cover located in more mesic ecosystems had higher soil C contents and basal microbial respiration rates that were associated with a greater likelihood of negative apparent priming effects (Figs. 2-4). *A priori*, the microbial community in these soils is expected to be adapted to greater C inputs from plants. In these communities, inputs of fresh substrate could be used by microbes to support growth, assimilating C in microbial biomass and thus limiting the release of CO_2 to the atmosphere, explaining the negative apparent priming effect in these soils. Conversely, our results suggest that positive apparent priming is likely greater in soils under drier climates (i.e. shrublands) and with land use (e.g., croplands) with low SOC contents[28,31] (Figs 1C and D, 2, and 3). A previous study using an herbaceous savannah soil, also revealed that positive priming effects were more likely to be observed in nutrient-limited soils[16]. The microbial community of these soils is likely not adapted to the input of fresh-organic C and might respond with an intense turnover to glucose addition. An additional

explanation can be the fact that some of these soils (i.e. soils under arid or semiarid climates) are not adapted to the soil water content utilized in the incubation (50% of the water-holding capacity) and microbial turnover could be stimulated in such conditions, contributing to the release of CO_2[48]. These findings have important implications for the future of C cycling in drylands, which are predicted to expand by up to 23% during this century [49], and cropping areas, which are expected to increase to support a growing human population.

Together, our work provides a comprehensive perspective on the ecological predictors underpinning the direction of apparent priming effects across a wide range of soils from different ecosystems and climates. The identification of the major ecological predictors of apparent soil priming across such a broad spatial scale and the consistency of variation for this phenomenon in an ecosystem-dependent manner, significantly improves our understanding of the potential turnover of microbial biomass and its contribution to CO_2 fluxes in soil. In agreement with the suggested hypothesis, our findings highlight the fact that the apparent priming effect is globally ubiquitous and controlled by the SOC content. Importantly, we place priming within an ecological context, showing that apparent soil priming is positive (accelerated microbial biomass turnover after glucose input) in soils with high aridity and relative abundance of *Basidiomycota*, and low plant cover, SOC content and basal microbial respiration rates. Further, our results indicate that salinity is an important negative driver of the apparent soil priming effect worldwide. These findings help elucidate the predictors of apparent soil priming in terrestrial ecosystems, with important implications for the study of C fluxes under forecasted climate change and for the improvement of global models of soil C dynamics. Further studies should extend the mechanistic understanding of priming, including more functional aspects of the microbial diversity (i.e. through the use of stable isotope labelling) and the chemical composition of organic matter, not only in terrestrial ecosystems, but also in aquatic ecosystems where priming effects also have been demonstrated to be important [10].

Methods

Soil sampling

Soil and vegetation data were collected between 2016 and 2017 from 86 locations in six continents (SI Appendix, Fig. S1). These locations include a wide range of globally distributed soil, vegetation (including grasslands, shrublands, forests and croplands) and climate (tropical, temperate, continental, polar and arid) types. Sampling was designed to obtain wide gradients of edaphic characteristics across soil formation stages while constraining climate[50,51]. Mean annual temperature ranged between -1.8 and 21.6 ºC, and Aridity Index between 0.08 and 4.33. Soils utilized in this study belong to a global collaborative network of soil chronosequences[52]. Field surveys were conducted according to a standardized sampling protocol[53]. In each location, we surveyed a 50 m × 50 m plot. Three parallel transects of the same length, spaced 25 m apart were added. The cover of perennial vegetation was measured in each transect using the line-intercept method[53]. Plant cover ranged between 0 and 100%. One composite topsoil (five 0-10 cm soil cores) sample was collected under the dominant ecosystem features across our plots (e.g., trees, shrubs, grasses, croplands). Following field sampling, soils were sieved (<2 mm) and frozen at -20 ºC.

Soil chemical and physical analyses

For all soil samples, we measured electrical conductivity, pH, texture, SOC content and available P (Olsen P) content. Soil properties were determined using standardized protocols[53]. Soil pH was measured in all the soil samples with a pH meter, in a 1: 2.5 mass: volume soil and water suspension. Soil texture (% of fine fractions: clay + silt) was determined according to Kettler et al. (2001)[54]. Total N was obtained using a CN analyzer (LECO CHN628 Series, LECO Corporation, St Joseph, MI USA). The content of Olsen P was determined from bicarbonate extracts using colorimetric analyses as explained in Olsen and Sommers (1982)[55]. SOC content ranged between 0.1 and 38%, available P between 0.5 to 72 mg P kg^{-1} soil, pH between 3.8 to 9.1 and the % of clay + silt varied between 0.3 and 86%, respectively.

Experimental incubation

As sugars are the most abundant organic C compounds in the biosphere and are presumably linked to priming effects[56], we use a low-molecular weight and highly available carbohydrate (glucose) as a trigger-molecule in our priming experimental incubations. Glucose is the most frequently released sugar during rhizodeposition[57] and a universal substrate for heterotrophic microbes. Given the wide spatial scale of our study, one sole source of a ubiquitous fresh organic matter (glucose) in one conventional dose was utilized. Glucose mineralization never reached 100% (always below 11% of the added glucose-C, Fig. S2) in any soil likely due to the capacity of organo-mineral complexes for stabilizing carbon into the soil[58]. Further, because plants were not used in the microcosms given the large variety of ecosystems, our simplified approach allowed us to remove the natural variation in root exudates and the consequent C inputs. Glucose was applied per soil weight, and not standardized by microbial biomass or SOC content. The reason is that our global survey includes soils with wide ranges in SOC and microbial biomass, but also in many other factors that can regulate the soil priming effect (i.e. clay content, available C content, plant and microbial communities, etc.)[7,17,18,24,45,59]. Thus, unlike in local studies where glucose addition can be standardized, we posit that the most reasonable approach to evaluate a priming effect at the global scale is adding glucose per unit of soil mass weight.

Two parallel sets of 1 g dry soil samples were placed in 20-ml glass vials at 50% of the water-holding capacity, sealed with a rubber septum and pre-incubated for one week at 28 ºC in the dark. During this time, microorganisms readapted to the water conditions and released a pulse of CO_2 due to the new moisture conditions[60]. Similar incubation times were utilized in other priming studies[18,61,62]. Subsequently, glass vials were opened and the atmosphere was refreshed. This standardization was necessary in order to homogenize conditions after the global sampling and storage at -20ºC. After the pre-incubation, glucose mineralization was assayed by adding ^{13}C-glucose (99 atom% U-^{13}C, Cambridge Isotope Laboratories, Tewksbury, Massachusetts, US) dissolved in water to one of the vial series at a dose of 240 µg of glucose-C per gram of soil. This dose was considerably high but in the range of previous priming studies and affect the growth and structure of the microbial community[14,24,57]. In parallel, the second sample set was subjected to the same procedure adding water without glucose; this sample set was used for measuring basal microbial respiration rates. A total of 172 incubations were conducted in this study (86 soils x two treatments). Then, soils were incubated for 16 days at 28ºC in the dark. Incubations were maintained for more than two weeks because previous studies have revealed that the major part of CO_2 release from soil tends to occur a few days or weeks

after substrate addition[7,]. Longer incubation time was not used as we want to avoid CO_2 saturation in the vials of C-rich soils. We are aware that our incubation conditions were outside the range for the mean temperature and water content of soils and, consequently, we estimated the potential apparent priming at the global scale. However, we were interested to know how soil edaphic conditions could influence the direction of apparent priming effects worldwide, and the legacy effects of climate (which would be modified by incubation conditions) are interpreted as indirect effects in our SEM, as discussed below. After incubation, 4 ml of headspace gas from each vial were transferred to pre-evacuated glass vials (Labco Limited, Lampeter, Wales, UK) and the quantity and isotopic composition of released CO_2 was then determined. The $\delta^{13}C$ isotope analysis was performed using a Thermo Scientific GasBench-PreCon trace gas system coupled to a Delta V Plus IRMS (Thermo Scientific, Bremen, Germany). The final delta values used for the ^{13}C calculations were expressed relative to international standards of V-PDB (Vienna Pee Dee Belemnite; [63]). The isotopic ratio of CO_2 was used to calculate the percentage of CO_2-C derived from the added glucose or from the soil [64]. Given the short-term nature of the incubation (16 days), the CO_2 release was interpreted as derived from the microbial biomass turnover, so called apparent priming effect[7-9]. This was defined as the increase or decrease in the CO_2 derived from the microbial biomass turnover following substrate addition. It was calculated as the total soil respiration following glucose addition minus the amount of C respired from the added ^{13}C-glucose and from control soil without glucose amendment [65]; Equation (3)). This was expressed as the extra CO_2-C (μg) released from soil.

$$\text{Priming effect} = (\text{total } CO_2 - \text{substrate derived } CO_2) - \text{total } CO_2 \qquad (1)$$

The first component (total CO_2 – substrate derived CO_2) refers to the soil amended with substrate and second component (total CO_2) refers to the unamended soil. Moreover, our metric of priming effect (μg CO_2-C g^{-1} soil day^{-1}) was strongly correlated with priming per unit of soil organic C (μg CO_2-C g^{-1} soil C day^{-1}; $\rho = 0.82$; $p < 0.001$; $n = 86$).

Microbial biomass and community composition

Microbial biomass was estimated using the substrate induced respiration approach using Microresp® as described in Campbell et al. (2003)[66]. The composition of bacterial and fungal communities was measured via amplicon sequencing using the Illumina MiSeq platform. Ten grams of frozen soil (per sample) were ground using a mortar and liquid nitrogen to homogenize soils and obtain a representative soil sample. Soil DNA was extracted using the Powersoil® DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. A portion of the bacterial 16S (V3-V4 region) and eukaryotic 18S (V9 region) rRNA genes was sequenced using the 341F/805R and Euk1391f/EukBr primer sets, respectively. Bioinformatic processing was performed using a combination of QIIME[67], USEARCH[68] and UNOISE3[69]. The relative abundance of microbial phyla was obtained from these analyses. 72/86 samples for fungi and 82/86 samples for bacteria were successfully sequenced and used for statistical analyses below. These samples include soils from all climates and ecosystem types.

Statistical analyses

PERMANOVA

We first tested for significant differences in priming effect across major ecosystem types using one-way non-parametric Permutational ANalysis Of Variance (PERMANOVA). In these PERMANOVA, each plot is considered a statistical replicate. Put simply, in our study we are using Earth as a grid across which we are collecting data from different plots or sites (replicates) from different ecosystem types. Having more than one sample within each plot would have been considered pseudo-replication as our question was related to comparing the priming effect across different ecosystem types globally (e.g., tropical vs. temperate forests) rather than comparing priming effect across plots within a given ecosystem type (e.g., two temperate forests). Further, gradient designs, as we have used, are powerful tools for detecting patterns in ecological responses to continuous and interacting environmental drivers as they generally outperform replicated designs in terms of prediction success of responses[70].

Structural Equation Modeling

We then used structural equation modeling (SEM)[35] to evaluate the direct and indirect relationships between abiotic (pH, salinity, SOC content, soil P content and texture), biotic (dominant vegetation types, plant cover, respiration rate, SIR-microbial biomass, and relative abundance of bacterial and fungal phyla) and climatic (MAT and aridity) environmental factors on apparent priming effect based on expectations of an *a priori* model (SI Appendix, Fig. S4). Due to the large number of potential microbial taxa predicting soil priming, prior to conducting the SEM, we first used Spearman correlations to identify a negative or positive correlation between the apparent priming and the relative abundance of microbial phyla. Only four taxa were significantly correlated with apparent soil priming (*Armatimonadetes*, *Verrucomicrobia*, *Basidiomycota* and *Chytridiomycota*; SI Appendix, Table S1); thus only these taxa were included in our SEM. Of these taxa, we found a significant effect of Basidiomycota only. Our SEM was conducted with the 69 soil samples including matching information for bacterial and fungal community composition. Climate factors (MAT and aridity) are used here as proxies of legacy effects, as incubations for priming effects are done under controlled laboratory conditions, with similar and constant soil water and temperature across all soils[27]. Because of this, we did not include the direct effect of climate on the apparent priming effects and respiration rates. However, we were interested in assessing the indirect effects of climate on priming *via* changes in SOC content and plant cover, aiming to provide an ecological context to our findings. After attaining a satisfactory model fit, we introduced composite variables into our model. The use of composite variables does not alter the underlying SEM model, but collapses the effects of multiple conceptually-related variables into a single composite effect, aiding interpretation of model results. Soil C and basal soil microbial respiration were included as a composite variable, because together they determine the amount of initial SOC content which is respired by microbial communities. Since some of the variables introduced were not normally distributed, the probability that a path coefficient differs from zero was tested using bootstrap tests. Bootstrapping tests do not in such cases assume that the data match a particular theoretical distribution.

Data availability

The complete dataset associated with this paper has been deposited in figshare: https://figshare.com/s/56430026ba793775983f (10.6084/m9.figshare.7054265).

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Author contributions

F.B and M.D-B designed the research and analyzed data. M.D-B. designed the field study and coordinated all field and laboratory operations. Field data were collected by all authors except N.F., P.T. and F.B. F.B and A.V performed laboratory incubations and calculated CO_2 fluxes, and M.D-B developed models in consultation with M.A.B. F.B, J.L.M, C.G and T.H contributed with reagents and materials. All the rest authors provided soil samples. The paper was written by F.B and M.D-B, edited by N.F., and the rest of the co-authors contributed to improve it.

Competing interests

The authors declare no conflict of interest.

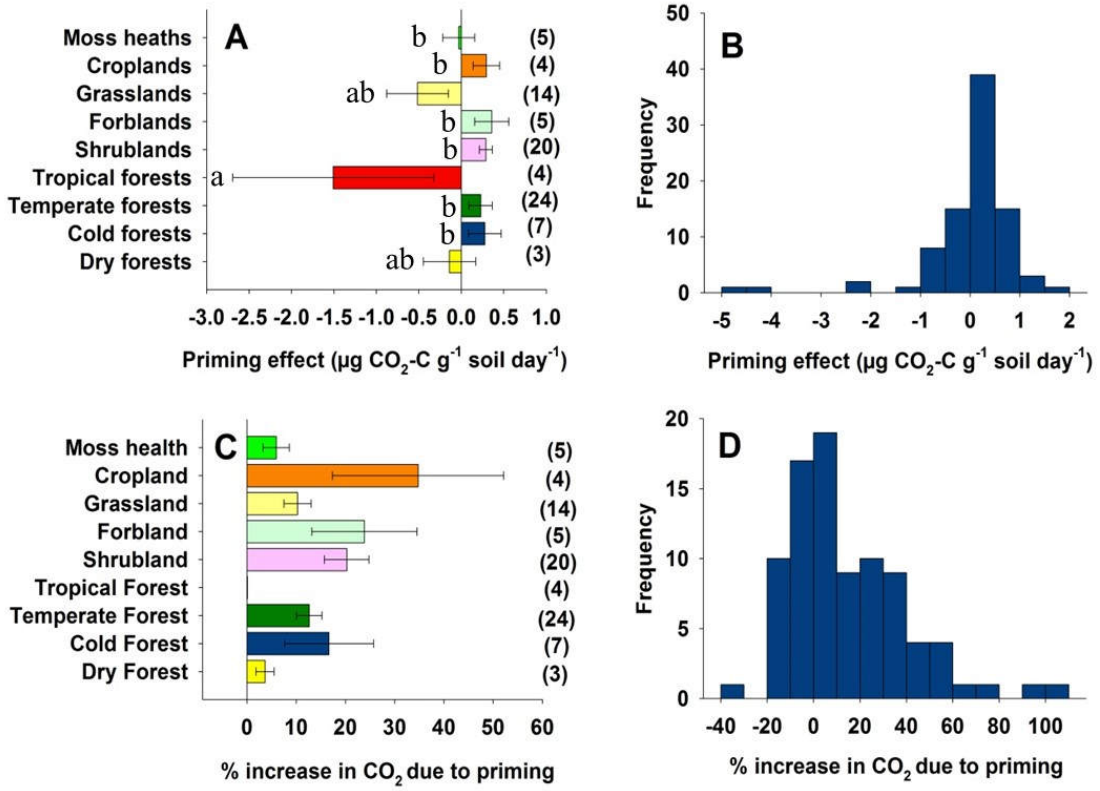


Figure 1. Apparent soil priming effects across globally distributed ecosystems. (A) Priming effect across major biomes. Different letters in this panel indicate significant differences among ecosystems (p = 0.007). (B) Histogram showing data distribution for the apparent priming effect. (C) Percentage of CO_2 from apparent priming *vs.* basal soil microbial respiration rates (p = 0.50). (D) Histogram showing data distribution for the apparent priming *vs.* soil respiration rates. Number of samples in brackets (n = 86). Ecosystems are defined using major vegetation types and the Koppen classification. Number of sites is indicated in parentheses. Error bars are standard error of the mean.

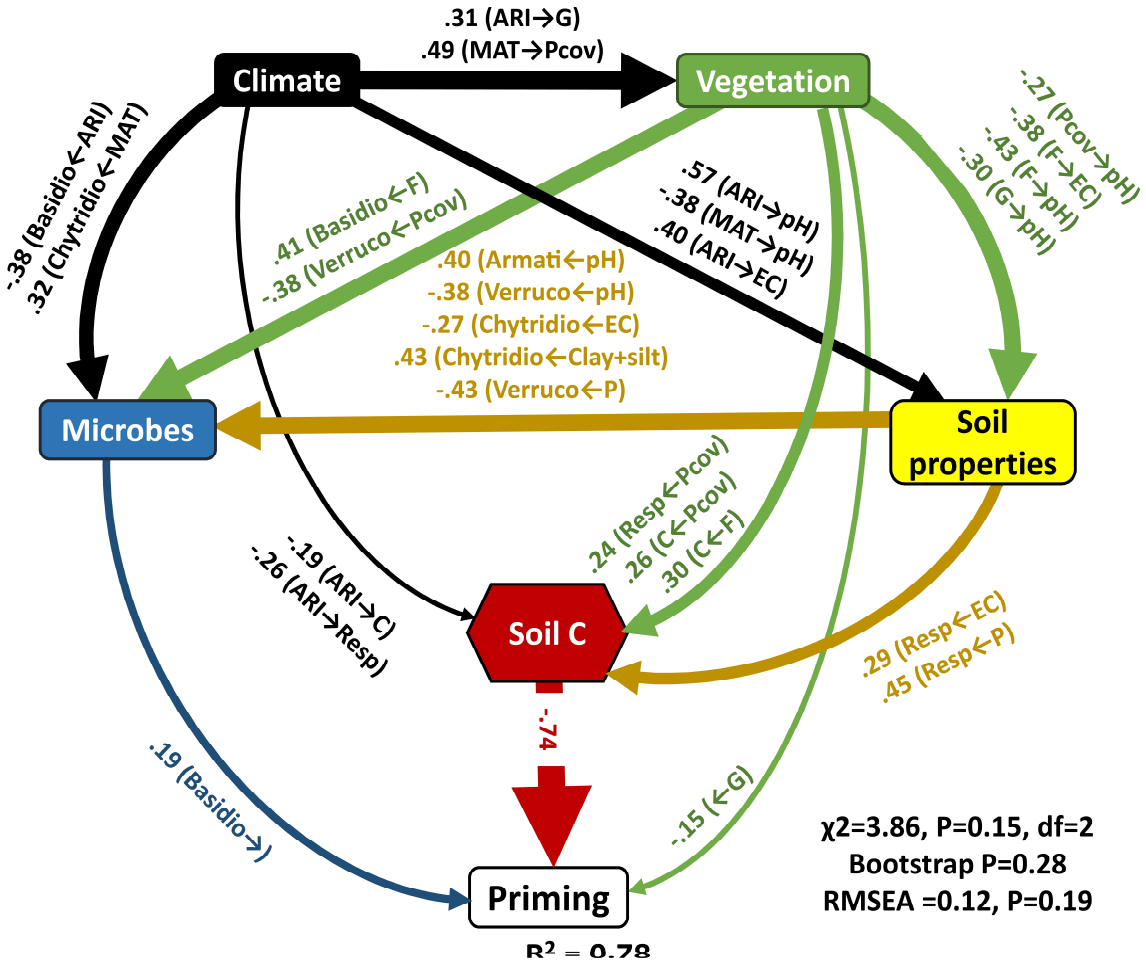
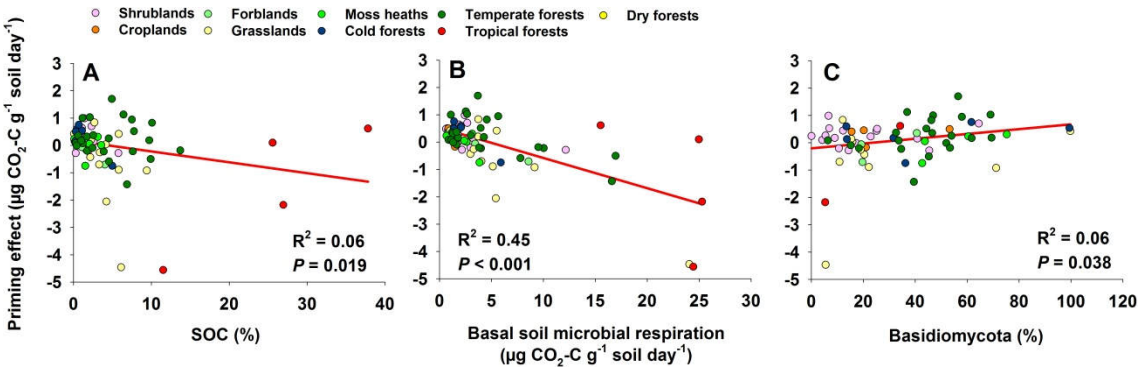


Figure 2. Ecological predictors of the apparent soil priming effect. Structural Equation Model (SEM) describing the effects of multiple ecological predictors on the apparent soil priming effect (n= 69). Numbers adjacent to arrows are indicative of the effect size ($p < 0.05$) of the relationship. R^2 denotes the proportion of variance explained. Climate, soil properties and vegetation predictors are included in our models as independent observable variables; however, we group them in the same box in the model for graphical simplicity. Soil carbon (C) associated variables (soil microbial respiration and soil organic C content) are included as a composite variable in our model (hexagon). F = forest. G = Grasslands. SHR = Shrublands. C+S = Clay + silt. EC = Salinity. Resp = Basal microbial soil respiration. Basidio = % of *Basidiomycota*. Verruco = % of *Verrucomicrobia*. Armati = % of *Armatimonadetes*. Chytridio = % of *Chytridiomycota*. Pcov = % of plant cover. ARI = Aridity (i.e., 1-ARI). Locations with a higher aridity also support lower water availability). MAT = Mean annual temperature. There was a non-significant deviation of the data from the model ($\chi2$ =3.97, df = 2; p = 0.14; RMSEA p = 0.18).



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771 **Figure 3.** Selected relationships from SEM between **apparent** priming effect and
772 environmental predictors.

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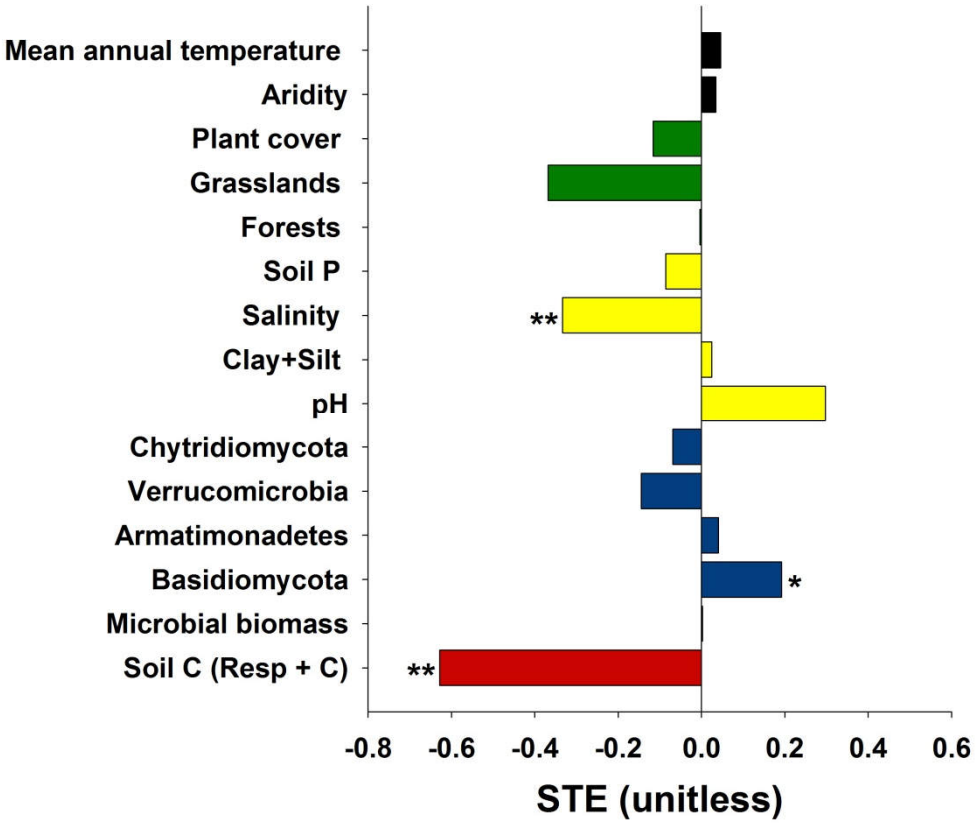

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786 **Figure 4. Standardized total effects (STE) from the Structural Equation Model**
787 **(SEM).** Sum of direct and indirect effects of multiple ecological predictors on the
788 apparent soil priming effect (n= 69). Soil carbon (C) represents the sum of the
789 standardized effect of soil organic C (SOC) and microbial respiration rates, which reflects
790 SOC which is respired by microbes. *$p < 0.05$, **$p < 0.01$.