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# Advancing the mechanistic understanding of the priming effect on soil organic matter mineralisation

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TITLE

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Advancing the mechanistic understanding of the priming effect on soil organic matter mineralisation

6 SUMMARY (320 Words)

8 1 The priming effect (PE) is a key mechanism contributing to the carbon balance of the soil 9 ecosystem. Almost 100 years of research since its discovery in 1926 have led to a rich body 10 of scientific publications to identify the drivers and mechanisms involved. A few review 11 articles have summarised the acquired knowledge; the last major one was published in 12 2010. Since then, knowledge on the soil microbial communities involved in PE and in PE + 13 C sequestration mechanisms has been considerably renewed.

- 142This article reviews current knowledge on soil PE to state to what extent new insights may15improve our ability to understand and predict the evolution of soil C stocks. We propose a16framework to unify the different concepts and terms that have emerged from the17international scientific community on this topic, report recent discoveries, and identify key18research needs.
- 19 3 Seventy percent of the studies on the soil PE were published in the last 10 years, illustrating 20 a renewed interest for PE, probably linked to the increased concern about the importance 21 of soil carbon for climate change and food security issues. Among all the drivers and 22 mechanisms proposed along with the different studies to explain PE, some are named 23 differently but actually refer to the same object. This overall introduces "artificial" 24 complexity for the mechanistic understanding of PE, and we propose a common, shared 25 terminology. Despite the remaining knowledge gaps, consistent progress has been 26 achieved to decipher the abiotic mechanisms underlying PE, together with the role of 27 enzymes and the identity of the microbial actors involved. However, including PE into 28 mechanistic models of SOM dynamics remains challenging as long as the mechanisms are 29 not fully understood. In the meantime, empirical alternatives are available that reproduce 30 observations accurately when calibration is robust.
- 31 4 Based on the current state of knowledge, we propose different scenarios depicting to what 32 extent PE may impact ecosystem services under climate change conditions.
- 3435 KEY WORDS
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37 Soil, Priming effect, Carbon cycle, minerals, enzymes, microbial actors, models, ecosystem services

#### 39 1 INTRODUCTION

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41 Soils host one of the main carbon (C) stores of our planet, around three times more than the 42 atmosphere does (2,400 vs. 800 GtC) (Friedlingstein et al., 2019). Most of this C is stored in organic 43 matter whose turnover controls soil fertility through the release of nutrients for plants. Soil Organic 44 Matter (SOM) also releases huge amounts of CO<sub>2</sub> into the atmosphere, 7-fold more than 45 anthropogenic emissions (Schlesinger and Andrews, 2000). Given the huge size of the soil organic C 46 pool, any change in the soil C content and its dynamics at a global scale – even if tiny – is associated to 47 great impacts in terms of food security and climate change (Dignac et al., 2017; Minasny et al., 2017). 48 Consequently, preserving and even increasing organic carbon in soils is of prime importance to meet 49 the food security challenge and mitigate greenhouse gas emissions (Minasny et al., 2017). This requires 50 getting insights into the determining mechanisms of the soil carbon balance – i.e. mineralisation vs. 51 sequestration.

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53 The priming effect (PE) is a key mechanism contributing to the ecosystem carbon balance (Fontaine et 54 al., 2007; Guenet et al., 2018). It corresponds to a change in the rate of SOM-C mineralisation by soil 55 microorganisms resulting from the input of fresh organic matter (FOM) (Bingeman et al., 1953). The 56 definition was later extended to almost any variation of microbial activities after an addition of 57 molecule (e.g., toxic compounds; Kuzyakov et al. 2000), but the present review will focus on C-related 58 PE as previously defined, and more precisely on the plant induced priming effect (PIPE) which includes 59 the rhizosphere priming effect (RPE) but also more generally all priming induced by plant originated 60 carbon inputs (Box 1). The PE occurs everywhere, but it has mainly been studied in soils (Bengtsson et 61 al., 2018; see supporting information). It has long been viewed as a net soil C loss since the most 62 frequent effect reported in the literature is a stimulation of native SOM mineralisation, up to 400 % 63 according to the type of environment and/or soil conditions (Guttière et al., 2021; Chen et al., 2019; 64 Perveen et al., 2019, Blagodatskaya & Kuzyakov, 2008). However, it can also be negative, with up to 65 50% reductions in soil carbon emissions (Lyu et al., 2018; Chen et al., 2019). As the PE is a complex 66 process, its impact on global C fluxes is hard to grasp and should be considered as a whole, integrating 67 feedbacks between the different and sometimes contrasting effects it causes: for example, the 68 increase of SOM mineralisation has negative consequences on climate change, and the nutrients 69 released from organic matter may be leached down the soil profile; but when the released nutrients 70 are taken up by plants, the PE indirectly contributes to plant growth and additional C sequestration in 71 the plant-soil system. Thus, the effect of PE variation on the net soil C balance is not trivial, particularly 72 in the context of climate change because C inputs may globally increase through enhanced plant

productivity, while soil C mineralisation may increase too due to higher temperature (Nishina et al., 2014). Consequently, better knowledge of the mechanisms involved in PE is of fundamental importance to improve our ability to control and predict the evolution of soil C stocks (Guenet et al., 2018; Chen et al., 2019), in agreement with the 2019 IPCC report on land (Shukla et al. 2019) that pointed out the need to better understand how PE will respond to climate change.

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79 Since the pioneering studies that evidenced it (Löhnis, 1926) and due to its importance for C cycling, 80 the PE has prompted a large body of research work to identify the drivers and mechanisms involved 81 (Kuzyakov et al., 2000; Blagodatskaya & Kuzyakov, 2008). A bibliometric analysis of the scientific 82 articles published in the field during the last 50 years shows however that 70% of all the articles are 83 recent, *i.e.* published during the last ten years, and mainly motivated by the rising concern about the 84 importance of soil carbon for climate change and food security issues. We provide as supplementary 85 information a brief report of the main outputs of this analysis highlighting the dynamics of publication, 86 the extent of the associated scientific network and the topical drivers of the publications 87 (Supplementary information available from Zenodo: https://doi.org/10.5281/zenodo.6326056).

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89 Based on these studies, it is clear today that the PE involves different microbial processes sometimes 90 driven in opposite ways by environmental parameters. Soil properties, climate, land use (Bastida et al., 91 2019; Siles et al., 2022), but also the nature of the substrates entering the soil (e.g., simple compounds, 92 complex compounds, plant residues or living roots) and the way they are added (e.g. continuous vs. 93 puse) all impact the intensity of priming effect. A few reviews have been published to summarise 94 knowledge in the field. The last major one was published in 2010 (Kuzyakov, 2010). However, in the 95 last ten years, studies aimed at characterising the microbial communities involved in soil processes 96 such as PE have benefited from considerable technical progress providing deeper insights into 97 microbial diversity and activity (Bouchez et al., 2016). In the same time span, the understanding of C 98 sequestration mechanisms has undergone a paradigm change (Lehmann & Kleber, 2015). Therefore, 99 it appeared important to update knowledge on PE mechanisms by integrating the findings of the last 100 10 years, which was the first objective of the present review. The second objective was to unify the 101 different concepts and terms that emerged from the international literature on this topic. Finally, we 102 identified and focused on specific points that need to be more deeply examined to evaluate and 103 predict the size and the impact of the different mechanisms across space and over time.

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105 2 UNIFYING THE DIFFERENT GENERATION MECHANISMS.

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107 A large number of mechanisms have been proposed to explain PE generation (Table 1). Some of them 108 are similar or even equivalent but have been named differently. This section (i) aims to clarify the 109 different denominations, (ii) groups them according to their effect on C fluxes, and (iii) integrates them 110 on a time scale. Box 1 gathers the terminology associated to the different pools of organic matter and 111 types of PE on which we based our discussion.

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2.1 Let's clarify the denomination of the different mechanisms.

114 The PE is usually measured as the difference between the CO<sub>2</sub>-C released from an amended soil 115 (excluding CO<sub>2</sub>-C originating from the amendment itself) and from a non-amended control soil over a 116 certain time period, leading to a "positive" or "negative" PE (Kuzyakov et al., 2000).

117 Negative PE have been attributed to "preferential FOM substrate utilization" by regular native SOM 118 decomposers (Cheng 1999). SOM decomposers can also switch from SOM decomposition to the 119 decomposition of FOM-decomposer necromass after intense predation (Cui et al. 2020). This process 120 has been called "necromass recycling" and also leads to reduced SOM decomposition and 121 mineralisation over time. Viral lysis has been suggested to generate more microbial necromass than 122 predation by protists or nematodes (Kuzyakov and Mason-Jones, 2018), but nobody has yet published 123 on the link between bacteriophages and PE.

124

Positive PE processes can be called "apparent" PE when they only result from the replacement of microbial cell C by C from the new substrate (labile fraction). Apparent PE have been described under 3 complementary processes (triggering effect, microbial activation, and pool substitution), depending on the amount of labile FOM added compared to the total microbial biomass (Blagodatskaya and Kuzyakov, 2008 – see Table 1).

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131 Real positive PE have been attributed to multiple processes. Those called "stoichiometric 132 decomposition" (Chen et al., 2014), and "mechanism 1" (Fontaine et al., 2003) refer to an acceleration 133 of SOM decomposition generated by the increase in extracellular enzymes produced by FOM 134 decomposers (Table 1). This implies that certain FOM and SOM compounds have chemical similarities 135 (e.g., a plant origin). Therefore, FOM should be at least partly polymerised (such as in residues, litter 136 or dead roots). Both processes occur when N is not limiting, but SOM catabolites benefit SOM 137 decomposers in "Mechanism 1", and FOM decomposers in "stoichiometric decomposition". Processes 138 called "N-mining" (Chen et al., 2014) and "mechanism 2" (Fontaine et al., 2003) result from the energy 139 brought by FOM catabolites, for SOM decomposers to break down biochemically recalcitrant SOM for 140 nutrients. For both processes, the targeted SOM pool was supposed to be also of plant origin. One process has been called "co-metabolism" in different papers and corresponds to the assimilation of FOM and SOM catabolites by either FOM or SOM decomposers, without being aimed at N acquisition (Kuzyakov, 2000; Yu et al., 2018). Therefore, in terms of carbon, this process overlaps with previouslydescribed mechanisms (either Mechanism 1 or Mechanism 2 and nutrient mining) and thus is not discriminant.

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A new mechanism of positive PE has been proposed recently to explain the rhizosphere PE (Keiluweit et al., 2015). Roots can exude organic acids, which cause the release of labile organic compounds from protective associations with minerals, and then these compounds can be decomposed by microbes. As a large part of this mineral-associated organic matter (MAOM) is derived from microbial necromass – with a low C:N ratio – through the so-called "entombing effect" (Liang et al., 2017), many nutrients, historically considered as a relatively passive reservoir, can be remobilised by this process, that we called "Abiotically mediated PE" (see section 3).

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2.2 Gathering mechanisms according to their effect on C fluxes

Two important parameters have to be considered to evaluate the impact of the different PE generation
 mechanisms on the dynamics and the fate of primed C.

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159 Firstly, native SOM is a mixture of different pools characterised by different turnover rates depending 160 on their biochemical nature and their accessibility to enzymes. The organic matter that enters the soil 161 is mainly of vegetal origin. Plant tissues are composed of molecules easily (hemicellulose, cellulose) or 162 less easily (lignins, polyphenols, phytates) broken down by microbial extracellular enzymes, hence fast 163 to medium-long turnover rates (a few days to a few years – Derrien et al., 2006). In contrast, the SOM 164 pools showing the lowest turnover rate (centuries) are composed of compounds from both plant and 165 microbial sources, protected from enzymes by mineral association (Lehman & Kleber, 2015). Carbon 166 primed from a SOM pool with a fast turnover rate should impact long-term carbon sequestration less 167 than C remobilised from a pool with a long residence time.

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Secondly, PE is often evaluated based on the change in CO<sub>2</sub> mineralisation rate, but respiration can be accompanied by incorporation of C into cell biomass (growth) (see Geyer et al., 2016 for a review). The efficiency of carbon incorporation into biomass (*i.e.*, carbon use efficiency, CUE) is calculated as the amount of microbial biomass produced *per* unit of resource consumed. The CUE of cells can vary between 0 (no growth but alive) to 0.85 (growth but still needing some energy for cell growth and maintenance) depending on their physiology and life strategy. The link between life strategy and CUE depends on the physiological status of microbes. R-strategists are actually less efficient than K- 176 strategists in using their assimilated C during a resting phase, due to a costlier basal metabolism. But 177 as these populations have higher maximal growth rates, during the growth phase when substrate is 178 not limiting, a higher proportion of C is allocated to biomass instead of respiration. This leads to a 179 globally higher CUE than that of K-strategists (Geyer et al., 2016). As PE generation mechanisms are 180 consequences of organic matter decomposition, they are more related to growth phases of different 181 populations than to their resting phases. Thus we consider that during a PE event, r-strategists have 182 high CUE while K-strategists have low CUE. Therefore, primed SOM assimilated by high-CUE 183 populations is likely converted into microbial biomass rather than mineralised into CO<sub>2</sub>, and further 184 stabilized via the so-called "entombing effect" (Lehman & Kleber, 2015; Liang et al., 2017). As a result, 185 high-CUE populations increase the chance of moving C from a fast- or a medium-turnover SOM pool 186 to a slow-turnover pool.

187

We classified the different processes proposed in the literature according to both previously-described parameters: the turnover rate of targeted SOM pool and the CUE of microbial populations assimilating its derived C (Table1). It is interesting to note that, to date, no study has revealed the SOM pool impacted by the negative PE.

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2.3 Time scale integration of PE generation mechanisms.

194 When FOM enters the soil, its nitrogen content will help cells synthesize new enzymes for further FOM 195 or SOM depolymerization. This phase of microbial turnover (apparent PE) first concerns high-CUE 196 microbial populations and low-CUE populations depending on the size of the labile fraction of FOM 197 (Figure 1). If the labile FOM pool exceeds the total microbial biomass and under non limiting N, SOM-198 decomposers will prefer the FOM substrate (negative PE) decreasing the regular SOM-C flux to the 199 atmosphere. If the labile FOM pool is exhausted before the available N, FOM decomposer exoenzymes, 200 liberated against the polymerized part of FOM will also attack SOM of vegetal origin. High-CUE 201 populations will be more competitive than low-CUE populations under such conditions and will 202 increase their biomass (stoichiometric PE). High-CUE population necromass will be rapidly recycled by 203 low-CUE populations or stabilised by mineral association (Figure 1). When the soil or FOM-available N 204 is exhausted, FOM catabolites will bring some energy to microbial populations able to catabolise 205 recalcitrant SOM for N (N-mining), or to dissociate N-rich SOM from minerals, both population types 206 having a low CUE. Nitrogen remobilised from SOM increases the soil nitrogen status and allows for a 207 next phase driven by high-CUE populations (Fang et al., 2018; Vain et al., 2021).

208 3 ABIOTICALLY MEDIATED PE: CONCEPTS AND MECHANISMS

210 3.1 Mineral-associated organic matter (MAOM)

In models of organo-mineral associations, mineral phases involved in organo-mineral associations can be classified into three main categories: well-crystallised minerals, short-range order phases, and metallic monomers. Each category is associated with a distinct conceptual model of organo-mineral association (Figure 2):

215 - Adsorption: organic molecules are adsorbed onto the mineral surface of well-crystallised minerals
 216 (e.g., smectite, vermiculite or goethite) (Kleber et al., 2007).

*Coprecipitation*: organic molecules are coprecipitated with short-range order phases or
 amorphous small polymers of Al, Fe and Si (Basile-Doelsch et al., 2015; Tamrat et al., 2019). Co precipitation is thought to be the dominant model as regards the amount of stabilised C
 (Rasmussen et al., 2018).

*Complexation and bridging*: organic molecules are bound to monomers (single ions). The main
 metals involved in complexation are Al and Fe in acidic soils. At higher pH, Ca dominates the
 organo-mineral associations by cation bridging (Rowley et al., 2018). Cations surrounded by
 organic molecules form a tertiary structure described as "supramolecular aggregates" (Sutton &
 Sposito, 2005).

The existence of these different types of organo-mineral models should be taken into account whenstudying MAOM in order to understand PE mechanisms.

228

229 In each type of organo-mineral association model described above, an additional degree of complexity 230 comes from the binding energies. Regardless of the model, the five following types of organic-inorganic 231 bonds can be present: covalent bonding, electrostatic cation bridges, hydrophobic interactions, Van 232 der Waals forces, and H bonding (von Lutzow et al., 2006). The binding strength varies very strongly 233 depending on the type of bond (Newcomb et al., 2017). Therefore, the energy required to break these 234 bonds and destabilise organic molecules is also a very important parameter in the control of the 235 MAOM PE. However, while this parameter seems thermodynamically easy to conceptualise, its 236 consideration in PE experiments is still in its infancy (Li et al., 2021).

237

The mineral-associated organic matter is less accessible but not fully inaccessible. The bonds between organic molecules and inorganic phases slow down OM degradation. Incubation studies have shown that MAOM is more difficult to mineralise than free OM, whatever the model (adsorption, coprecipitation or complexation) (*e.g.* Jones & Edwards, 1998; Saidy et al., 2015). The proportion of C mineralised during MAOM incubations reached a plateau which, depending on the compounds, barely reached the same proportion as in the control where OM was not associated with mineral phases. These experiments showed that (i) part of MAOM remained accessible to microorganisms but mineralisation was slowed down, and (ii) depending on the nature of the organic compounds and the nature of the mineral (*i.e.*, depending on the nature of the chemical bond), part of MOAM was not mineralised by microorganisms. Thus, rather than use a binary terminology tending to say that OM is stabilised or not in organo-mineral associations, a stabilisation gradient concept should be preferred and considered as a key parameter driving the potential of abiotically mediated PE.

250 3.2. Priming effect of mineral-associated organic matter

The above-mentioned experiments did not take the full complexity of soil functioning into account. When the physicochemical conditions of the soil solution are modified (changes in pH, redox conditions, ionic strength, composition), the speciation of the mineral phases and organic molecules can be modified, leading to an altered configuration of organo-mineral associations. During these changes, if OM becomes more easily accessible to microbial enzymes, accelerated decomposition (*i.e.*, a PE) may be observed.

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258 The biotic impact on the physico-chemical parameters of MAOM leads to a direct and indirect PE 259 pathways. Roots and microorganisms play an essential role in controlling the physicochemical 260 conditions of the soil solution (Figure 2). Multiple factors impact these conditions. For example, 261 vascular plant roots, fungi and bacteria release low-molecular-weight organic acids. These are mainly 262 carboxylic acids like formic, oxalic, and acetic acid, but also aliphatic and aromatic acids (Clarholm et 263 al., 2015 and references therein). Microorganisms may decrease the pH locally in microsites 264 (Bonneville et al., 2011). Roots also release some easily metabolisable simple sugars (e.g., glucose). 265 They can stimulate microbial activity and growth, which may in turn lower the pH and the redox 266 potential (Mabuza et al., 2020). These various examples show that the factors driving the 267 destabilisation of MAOM are multiple and may be dependent on each other. The factors directly 268 controlled by plant functioning are referred to as "direct (non-microbial) pathways". Conversely, in 269 "indirect (microbial) pathways" root exudates mobilise MAOM indirectly through a sugar-mediated 270 pathway dependent on microbial intermediaries (Keiluweit et al., 2015; Jilling 2021; Finley et al., 2018; 271 Li et al., 2021). Whether the pathway is direct or indirect, whether it is located in the rhizosphere or in 272 the residuesphere, it appears that the functioning of the biotic compartment (roots, bacteria and fungi) 273 is a source of low-molecular-mass organic acids, and pH and Eh variations, all of which are likely to 274 modify the bonding equilibrium of the organo-mineral associations and can be accompanied by an 275 abiotically mediated PE.

The conceptual mechanisms of abiotically mediated PE include three types of reactions releasing mineral-bound C and making the compounds accessible to the extracellular enzymes of microorganisms (Figure 2):

*Mineral dissolution* can be promoted by exudates. Ligand-promoted dissolution is accelerated by
 strong ligands such as organic acids (Wang et al., 2014; Li et al., 2018). Protonation of a mineral
 surface can also weaken metal-oxygen bonds and dissolve minerals (Stumm, 1997). Reductive
 dissolution can be driven by organic reducing agents such as phenols and aromatic acids
 (Vermeire et al., 2019). However, as Al is not very sensitive to redox variation, these redox
 processes mainly impact Fe-bearing mineral phases.

*Replacement* is promoted by strong ligands such as organic acids, which sorb onto mineral surfaces and displace or release previously sorbed organic compounds from minerals (Li et al., 2021). Other metabolites are also implied in the release of MAOM through displacement of weakly bound compounds (Leineman et al., 2018; Mikutta et al., 2019; Jiang et al., 2021).

*Direct depolymerisation* of mineral-bound organic compounds by extracellular enzymes can also
 occur on weakly bound OM, bypassing the desorption step (Wang et al., 2020).

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293 4 ROLE OF ENZYMES IN PE

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#### 4.1 Enzymes involved in priming effect mechanisms

296 The type of enzyme involved in PE depends on (i) the chemical composition of the added substrate, (ii) 297 the chemical composition of the native SOM, (iii) the nutrient availability, and (iv) the functional 298 requirements of microorganisms, which differ amongst microbial communities. When the 299 environment is not nutrient limited, FOM input is expected to increase the activity and biomass of 300 high-CUE microbial communities presenting a high growth yield due to an increased activity of the 301 FOM depolymerizing enzymes (Fanin et al., 2014; Fanin & Bertrand, 2016; Malik et al., 2019). For 302 example, additions of plant residues stimulate plant cell-wall-degrading hydrolytic enzymes, and the 303 resulting PE is directly related to enhanced degradation of plant-derived residues of the native SOM 304 (Chen et al., 2014). Increased activity of microbial communities can also enhance the degradation of 305 native SOM as a result of co-metabolism, *i.e.*, hydrolase activity yields enough energy and monomers 306 to produce a panel of other enzymes degrading FOM, or/and the non-complex and accessible SOM 307 (Blagodatskaya & Kuzyakov, 2008; Pascault et al., 2013).

When the environment is nutrient limited, microbial communities shift from high to low CUE, notably because nutrient limitation affects the community metabolism and reduces growth yield, while it favours investment in resource acquisition (Malik et al., 2020; Fanin et al., 2020). In this context, another type of co-metabolism directed to N-containing SOM is induced when N is not available or becomes exhausted at the late stages of decomposition. It is characterised by a high expression level of enzymes degrading N-containing compounds (Moorhead & Sinsabaugh, 2006; Chen et al., 2014), including hydrolytic chitinases and oxidases, which release N associated to complex aromatic compounds (Derrien et al., 2014). The resulting PE is directly related to enhanced degradation of Nrich SOM compounds that differ chemically from those of the added substrate.

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#### 4.2 Energy cost and return on investment

319 The activity of enzymes involved in PE implies benefits and costs. The major benefit from enzyme 320 activity is the release of mineral nutrients and organic monomers and oligomers that can be taken up 321 and assimilated by microbes. On the other hand, the costs of enzyme production include the C and 322 nutrients necessary to build the backbone structure of the enzyme itself, but also the metabolic energy 323 required for protein synthesis and enzyme excretion (Allison et al. 2014). Because extracellular 324 enzymes have a short lifespan, a return on investment is necessary to maintain microbial growth, 325 especially when resources are scarce in the environment. Nevertheless, the impact of the energy 326 balance associated to enzymes involved in PE is still unknown.

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329 A critical factor influencing the energy balance related to enzymes is the distance between the 330 substrate and the enzyme producer. While some enzymes are directly attached to the plasma 331 membrane of microbial cells or grouped into multi-enzyme complexes (named 'membrane enzymes' 332 hereafter), like the cellulosomes dedicated to cellulose degradation, other enzymes are excreted far 333 away from the cells (named 'exoenzymes' hereafter). When microbes are relatively near their 334 substrates, the monomers produced by membrane enzymes are directly recognised by cell-wall 335 receptors and transported into microbial cells, and this optimises resource uptake from the soil 336 solution. The benefits of enzyme production often exceed the costs thanks to a high return on 337 investment, and allow for microbial growth (Schimel & Weintraub, 2003). By contrast, exoenzymes are 338 sent far away from microbial cells, up to a few mm (Gaillard et al., 1999; Poll et al., 2006; Védère et al., 339 2020). A significant portion of labile C released through enzymatic action may be lost to the enzyme 340 producer (*i.e.*, leached to deeper soil horizons, immobilised in soil aggregates and/or taken up by other 341 microorganisms) (Allison, 2005; Burns et al., 2013). As a consequence, microbes may invest in chemical 342 defenses (i.e., antibiotics) or produce more enzymes to optimize enzyme foraging (Hiscox & Boddy, 343 2017).

For these reasons, the degradation of substrates by membrane enzymes may potentially have a stronger positive feedback on SOM decomposition and biomass growth (and thus on PE) than exoenzymes. Therefore, we propose that the distance between microbes and their substrates as well

347 as substrate accessibility to enzymes should be considered as primary factors driving the magnitude 348 of PE across various soil types. This could be tested by implementing random mutagenesis, gene 349 complementation and functional assays (as performed by Picard et al., 2021) to identify how any 350 mutation affecting the production of membrane-cellulosomes or exo-cellulases of a microbe 351 community inoculated on a sterile soil impacts SOM decomposition and microbial growth after the 352 addition of cellulose. Batch experiments with spatially localized applications of decomposers and of 353 fresh cellulose on a sterile soil (as performed by Pinhero et al., 2015) could also allow the investigation 354 of the effect of varying distances between substrate and decomposers on PE intensity.

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#### 4.3 PE induced by enzymes sorbed to minerals

Exoenzymes circulating in soil pores exhibit a strong affinity for mineral surfaces and can sorb onto them (Olagoke et al., 2019; Olagoke et al., 2020). This mechanism protects them from degradation and accounts for their persistence in the soil. Mineral-associated exoenzymes are suspected to contribute to the depolymerisation of freshly added substrate, even if their activity is diminished due to changes in conformation after binding to mineral surfaces. They are beneficial to the cost:benefit ratio of the PE because the released monomers are cost-free for the microorganisms that assimilate them.

The monomers taken up into microbe cells are either directed towards microbial biosynthesis, or oxidised into CO<sub>2</sub> by endoenzymes, as reported by CUE. Under aerobic conditions, the aerobic oxidation of monomers also generates energy in the form of adenosine triphosphate. Endoenzymes may be involved in a PE when they are released from dead microbial cells, attached to mineral surfaces, and maintained their activity outside the cell, with electron transfer to O<sub>2</sub> potentially ensured by soil particles due to their electric charge (Maire et al., 2013; Trevors et al., 1982).

- 369
- 370 5 MICROBIAL ACTORS OF PE
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#### 5.1 Actors proposed in the literature

373 Using molecular approaches, various studies have linked certain PE generation mechanisms to specific374 bacterial or fungal taxonomic groups listed in Table 2.

Bacterial taxa have been much better documented than fungal ones, probably because of methodological limitations. While a hyphal section is at the microbial scale, its prospected soil volume exceeds the cubic meter. Therefore, current molecular techniques are better adapted to single cell microbial populations (Ranjard et al., 2003). Yet, saprotrophic fungi are believed to have a preponderant role in PE generation, especially in the N-mining process. Their hyphal physiognomy allows them to co-metabolise FOM and SOM very easily, and they appear to be more competitive than bacteria for cellulose decomposition and in turn use cellulose C as an energy source for N-mining. In addition, some fungi have strong enzymatic capacities to break down recalcitrant compounds and
 access trapped N (Fontaine et al., 2011).

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Kingdom or phylum levels do not seem appropriate to associate taxa to specific PE generation mechanisms. Bacterial and fungal taxa have been assigned to all the different PE generation mechanisms (Table 2). Bacteria are roughly considered as r-strategists and fungi as K-strategists, but the reality is more complex (Ho et al., 2017; Tardy et al., 2015). The genus level shows a better correspondence except for *Bacillus*, which gathers both true oligotrophic (*i.e.*, K-strategist) and copiotrophic (*i.e.*, r-strategist) species (Morrissey et al., 2017).

391

392 Some interpretations have suffered from a lack of knowledge on poorly described phyla like the 393 Gemmatimonadetes, classified as oligotrophic by some authors (Pascault et al., 2013) but copiotrophic 394 by others (Yu et al., 2020). Increasing efforts in culturomics (Sarhana et al. 2019) and also in large-scale 395 studies of soil microbial diversity will provide precious information to confer functional attributes to 396 microbial taxa (Karimi et al., 2018).

397

The r-to-K or oligotroph-to-copiotroph concepts refer to a continuum, and many central taxa can develop a certain physiological flexibility depending on (i) environmental conditions, and (ii) competition or complementarity with the other taxa present in each assemblage. These taxa can therefore participate to different PE generation mechanisms according to local conditions (Bernard et al., 2009).

403

#### 404 5.2. A trait-based approach

405 Proposing taxa associated with the different PE generation mechanisms requires to directly focus on 406 functional traits linked to the different PE generation mechanisms described so far. Data retrieved 407 from the application of -omics techniques to environmental samples and recent developments in 408 culturomics have provided and will continue to provide precious information about the genes and 409 enzymes associated with particular taxa.

410

Different bacterial genomic traits have been proposed to be related to maximum growth rates, and therefore to maximal CUE (linked to stoichiometric decomposition PE), like a high copy number of the ribosomal operon (Klappenbach et al., 2000), a small genome size (Saifuddin et al., 2019), vicinity of the ribosomal operon and the chromosomal origin of replication (Viera-Silva & Rocha, 2010), and the translation efficiency, (Weissman et al., 2021). Some genera sharing those traits are *Burkholderia* sp., *Flavobacterium* sp. and some *Bacillus* sp. (Fierer et al., 2017). The highest maximal fungal growth rates are shared by some well-known saprotrophic fungi that solely use simple sugars and produce spores
(Ho et al., 2017), like Acremonium, Alternaria, Aureobasidium, Cladosporium, Cephalotrichum, Mucor, *Rhizopus*, and *Thysanophora*. Decomposition of polymers like cellulose and chitin is widespread and
shared by copiotrophic bacterial and fungal species. Genes associated to simple sugar metabolism and
β-glucosidase activity were recently shown to drive PE in forest soils (Ren et al., 2021).

423 Obligate low-CUE bacteria should be characterised by opposite genomic traits, as adapted to 424 oligotrophy by adopting a small size, a high adsorption capacity of substrate monomers. They should 425 not produce depolymerising enzymes because maintaining these genes is costly (Lynch & Marinov 426 2015). Therefore, key species implied in nutrient-mining PE should first share a high diversity of genes 427 coding for acquisition systems of poorly accessible substrates. White- and brown-rot saprotrophic 428 fungi and certain bacterial species (Nocardia sp., Streptomyces viridosporum and other sp., 429 Amycolatopsis sp., Xanthomonas sp., Rhodococcus jostii., Novosphingobium sp. and Sphingomonas 430 sp.) share various peroxidases and laccases (Brown & Chang, 2014). All these bacterial genera have 431 between 2 6 copies of the ribosomal in and operon their genomes 432 (https://rrndb.umms.med.umich.edu), suggesting that they can be physiologically flexible and adapt 433 their CUE to the quality of the substrates they are decomposing. This is also the case of bacterial and 434 fungal species able to weather minerals by producing ligands or chelating agents and who might be 435 good candidates for the abiotically mediated PE, like Arthrobacter, Janthinobacterium, Leifsonia, 436 Polaromonas and Burkholderia (see Uroz et al., 2015 for a review). As phosphorus and organic matter 437 compete for sorption sites on minerals (Spohn et al. 2022), P-solubilising bacteria could also have an 438 effect on SOM sorption. Bacillus subtilis can desorb P from gibbsite by mineral adhesion of the cells 439 themselves (Hong et al., 2016).

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#### 6 HOW TO INTRODUCE PE INTO MODELS

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443 Priming is difficult to model, like any other observed but not fully understood phenomenon. To 444 develop a mechanistic model, equations describing the phenomenon are needed, and the very first 445 step is obviously an in-depth understanding of observations. With priming, the situation is somehow 446 slightly uncomfortable for modellers because the debate about the drivers of priming is still ongoing 447 (Chen et al., 2014). Nevertheless, the ubiquity of priming and its potential importance in the soil C 448 balance in a climate change context (Terrer et al., 2021) urge modellers to include priming in their 449 models. We can basically split the modelling objective related to priming into two categories, *i.e.*, (i) 450 understanding the phenomenon, and (ii) quantifying it because observations have shown that 451 priming plays a major role in the C balance of ecosystems. Both objectives can be considered as

independent or linked depending on the authors (Blagodatsky et al., 2010; Guenet et al., 2018; Neill
& Gignoux, 2006; Perveen et al., 2014). These categories are often associated with different spatiotemporal scales (Figure 3): most of the models aim at understanding priming at small scales and over
short time periods, whereas models aimed at quantifying the importance of priming on the SOM
balance are developed at larger scales and over longer time periods.

457

458 Priming being defined as a change in the SOM mineralisation rate induced by FOM additions 459 (Kuzyakov et al., 2000), we can consider that classic models describing SOM mineralisation using first-460 order kinetics – e.g., CENTURY or RothC (Coleman et al., 1997; Parton et al., 1987) – implicitly include 461 priming in their decomposition parameter values. Nevertheless, this is associated with implicit 462 assumptions that the relative importance of priming is fixed in space and over time. In particular, an 463 important implicit assumption of first-order kinetic models is that the microbial community is stable. 464 This hypothesis is not verified in a context of global change (climate,  $CO_2$  + land use) (Carney et al., 465 2007), and priming will play a major role on future C balances (Terrer et al., 2021). Therefore, it is 466 necessary to understand and quantify priming to represent it in models instead of just considering it 467 implicitly.

468

469 To represent priming following the classic definition, the FOM and SOM compartments must interact 470 directly or indirectly. This can be done simply by implementing SOM rate modifiers depending on 471 FOM (Guenet et al., 2013) or by changing the SOM CUE according to FOM availability without 472 modifying the decomposition rate (Zhang et al., 2018). Priming can also be represented by models 473 that consider explicit microbial mechanisms, with the effect of FOM on SOM considered through 474 microbial biomass (Fontaine & Barot, 2005; Huang et al., 2018; Perveen et al., 2014; Wieder et al., 475 2015). These different views on priming representation in models should not be seen as 476 contradictory or opposed, but complementary. It would be unrealistic to consider that a complete 477 representation of priming will soon be included in large-scale models (Eyring et al., 2016); simple and 478 semi-empirical approaches are needed. However, it would also be quite unrealistic to believe that 479 semi-empirical approaches will help to develop a deep understanding of priming. In our opinion, the 480 main difficulty in both cases is related to the parameters used in the equation. Increasing model 481 complexity is most often associated with an increased number of parameters and reduced linear 482 responses of the models (Huang et al., 2021). Therefore, the more complex a model is, the higher 483 the number of possible model trajectories. To avoid unrealistic model behaviors, it is of prime 484 importance to constrain the model parameters using observations. Complex models associated with 485 short time periods and small scales can be constrained by observations coming from incubations 486 under controlled conditions (Neill & Guenet, 2010). Nevertheless, applying complex models and 487 finding suitable parameter values for different soil types, climates, plant covers, etc. is an important 488 challenge that requires a large dataset of incubations like those recently published by Bastida et al. 489 (2019). Even though such large datasets of incubations are now published in single studies or in meta-490 analyses (Luo et al., 2016), laboratory incubations are still carried out in controlled environments, 491 and upscaling the parameters obtained at this scale to the ecosystem or even the global level is not 492 straightforward. At the end of the calibration process, upscaling may increase model prediction 493 uncertainties compared to less mechanistic models because the uncertainties associated with 494 parameter estimation and upscaling are large. Semi-empirical approaches with a limited number of 495 parameters are an intermediate approach that make it possible to add priming explicitly and to study 496 its effect at larger scales (Guenet et al., 2016; Perveen et al., 2014; Sulman et al., 2014). These models 497 do not catch the entire complexity of the priming response, but they are robust enough to estimate 498 the importance of priming on the SOM balance at large scales.

499

500 Different models may involve different, equally accurate or equally uncertain approaches. Therefore, 501 uncertainty remains concerning our prediction capacities. To solve this problem, a promising 502 approach consists in working in close collaboration with experimenters to set up trials aimed at 503 better understanding priming, developing the associated equations and estimating the parameters. 504 But current models can also be compared in the short term. This approach has been fruitful in many 505 fields such as climate sciences (IPCC 2013), biogeochemistry applied to large scales (Ito et al., 2020), 506 and SOM dynamics (Farina et al., 2021). Therefore, using model intercomparison exercises is an 507 interesting alternative to provide robust estimations. This is particularly important when such 508 estimations are key information for stakeholders and policy makers and robust estimations by soil 509 scientists are expected in the near future (Shukla et al., 2019).

510

511 Another difficulty in including priming into large-scale models representing plant growth and 512 phenology, water cycles and energy fluxes (Cramer et al., 2001; Sitch et al., 2003) is related to the 513 feedbacks between all the model (Goll et al., 2014; Zaehle et al., 2010; Zhu et al., 2019). A promising 514 research avenue aiming to incorporate complex models with reduced feedbacks but not yet 515 implemented in soil science to our knowledge is the use of a model emulator (Fer et al., 2018). Such 516 approach can help large-scale models to consider priming based on a complex mechanistic approach. 517 Representing priming in models is still a challenge with a large diversity of approaches that should 518 be considered as complementary and able to tackle highly different situations, from a deep 519 understanding of priming at small scales to the quantification of the importance of priming in the 520 global C budget.

522 523 7

#### CONSEQUENCES OF PE ON ECOSYSTEM SERVICES UNDER GLOBAL CHANGE CONDITIONS

524 Due to various technical constraints related to the measurement of PE such as isotopic labelling of 525 contributed OM, PE studies are often conducted in the laboratory in soil incubations with pure 526 chemical compounds (e.g., glucose) making any extrapolation to the ecosystem scale very 527 complicated. However, some studies have quantified PE and its impacts on C and N fluxes in soil-plant 528 systems (see review of Cheng et al., 2014), often involving heavy infrastructure in order to guarantee 529 the reliability of measurements (Cros et al., 2019). These studies show a massive change in SOM 530 decomposition rate in their rhizosphere induced by plants, from a 50% reduction to a 280% increase 531 (Cheng et al., 2014; Huo et al., 2017). This plant induced priming effect (PIPE) results from the 532 combination of several rhizosphere processes such as plant C inputs (litter rhizodepositions) as well as 533 root uptake of nutrients and water intensifying drying-rewetting cycles and breakage of soil aggregates 534 (Dijkstra et al., 2021). Most if not all ecosystem services and disservices related to SOM dynamics are 535 impacted by the PIPE. For example, the PIPE has been suggested to increase disservices such as soil C 536 loss (Carney et al., 2007; Henneron et al., 2020a) and nitrate leaching (Liu et al., 2008), as well as 537 services such as soluble nutrient supply to plants sustaining greater plant production and CO<sub>2</sub> fixation 538 (Henneron et al., 2020a; 2020b).

539

540 Understanding the response of the PIPE and SOM dynamics to current global environmental changes 541 (atmospheric CO<sub>2</sub> increase, global warming and land use changes) is crucial to predict the long-term 542 evolution of the related (dis)services. The task appears very complex because global change can act on 543 priming processes in multiple ways. For example, global warming can impact the intensity of PIPE 544 through its effects on soil enzyme activity, soil microbial populations (Fanin *et al*. in this Special Issue) 545 and plant communities, and in turn determine the quantity and quality of plant C inputs into soils. This 546 complexity is increased by the fact that other processes than PIPE control SOM dynamics (e.g., SOM 547 formation) and have their own response to global change. We suggest a framework that reduces this 548 complexity to three scenarios describing the effect of GC on PIPE, SOM dynamics and four ecosystem 549 (dis)services (Figure 4). This framework is based on the assumptions that (i) plants can drive SOM 550 dynamics to meet their soluble nutrient needs, and (ii) global change can degrade this effect.

551

It is increasingly recognised that plants can modulate the PIPE and SOM dynamics to adjust the microbial supply of soluble nutrients to their demand. In a common garden experiment comparing 12 grassland plant species, SOM mineralisation rates have been found to be adjusted to the demand of each species (Henneron et al., 2020b). Enhanced plant photosynthesis and nutrient demand under elevated CO<sub>2</sub> increase the PIPE, soil organic N mineralisation and plant N uptake in many different

557 contexts (de Graaff et al., 2009; Kuzyakov, 2019). In contrast, decreased plant photosynthesis (plant 558 demand) in response to plant shading/cutting induces reduced SOM mineralisation (Shahzad et al., 559 2012; Tang et al., 2019). In temperate ecosystems, the mineralisation/immobilisation ratio changes 560 throughout the season in line with plant demands; immobilisation dominates in winter (low demand), 561 whereas mineralisation dominates in spring (high demand) (Bardgett et al., 2005; Yokobe et al., 2018). 562 Plants control the storage and release of C and nutrients from SOM through their C inputs and soluble 563 nutrient uptake, and this alters the activity of high-CUE and low-CUE microbes (Figure 5). Based on this 564 knowledge on plant control of SOM dynamics, our framework suggests three scenarios of ecosystem 565 response to global change. These scenarios should be considered as attempts to summarise current 566 knowledge, to make it easier to include PE in models and identify priorities for further investigations 567 on the effects of global change on ecosystem C and nutrient cycles.

568

569 Scenario 1: Control by plants is maintained – Global change affects plant production. The effects of 570 GC on plant-soil systems are moderate in that plants keep their ability to adjust SOM dynamics to their 571 nutrient needs. Therefore, the ecosystem response to global change is determined by the plant 572 response to global change. More specifically, plant production is modified by global change, while 573 plant biomass remains unchanged. For example, in grasslands under elevated CO<sub>2</sub>, primary production 574 is strongly stimulated but the amounts of C and nutrients stored in plant biomass barely change (Terrer 575 et al., 2021) as a consequence of the low storage capacity of herbaceous plants (compared to trees) 576 and continuous grazing. Our framework suggests that the change in primary production modifies the 577 turnover rate of SOM, not the SOM stock. The higher (or lower) plant nutrient demand is expected to 578 increase (or decrease) PIPE and SOM mineralisation. However, an equivalent amount of organic 579 nutrients is expected to return to the soil through litter fall and rhizodeposition if no biomass is 580 exported; this replenishes the SOM stock during periods of low plant demand (Figure 5). In sum, the 581 soil C and ecosystem C stocks as well as nutrient losses remain unchanged, while plant production is 582 changed, meaning there is no feedback effect on global change.

583

584 Scenario 2: Control by plants is maintained - Global change affects standing biomass. The sole 585 difference with scenario 1 is that global change also affects the standing plant biomass, as in forests 586 submitted to elevated  $CO_2$  or moderate warming (+ 1 or 2 °C) where primary production and tree 587 biomass often increase (Melillo et al., 2002; Terrer et al., 2021). The increase or decrease in plant 588 biomass induces a parallel and opposite change in the SOM stock (a decrease or an increase, 589 respectively). Given that plants drive the PIPE and SOM dynamics as a function of their nutrient 590 demand, SOM behaves as a nutrient source or sink according to whether plant biomass accumulates 591 or loses nutrients. This nutrient redistribution between plant biomass and SOM affects the ecosystem 592 C stock since these two compartments have different carbon:nutrient ratios (*e.g.*, redistribution of 593 nutrients towards plant biomass increases ecosystem C). In sum, plant production, the soil C stock and 594 the ecosystem are modified, while nutrient loss remains unchanged. In other words, an increase in 595 plant biomass leads to negative feedback and therefore attenuation of climate change, whereas a 596 decrease in plant biomass leads to a runaway positive feedback on climate change.

597

598 Scenario 3: Global change degrades plant control of SOM dynamics. This scenario considers more 599 extreme impacts of global change on plant-soil systems leading to a partial or total degradation of the 600 control of SOM dynamics by plants. For example, extreme climatic events such as droughts or 601 heatwaves can block plant nutrient uptake while soil microbes continue to mineralise SOM and release 602 soluble N that accumulates in soils (Deng et al., 2021). Degradation of plant control of the PIPE and 603 SOM dynamics leads to periods of excess soluble nutrients on the short term; these excess nutrients 604 increase nutrient loss and environmental pollution, and periods of nutrient deficiency limit plant 605 production. On the long term, the increased nutrient loss contributes to progressive soil 606 impoverishment and ecosystem decline (loss of plant biomass and production, lower ecosystem C 607 stock). This scenario leads to a runaway positive feedback on global change (climate change and 608 disruption of nutrient cycles)

609

610 Several experimental studies support our scenarios. The higher plant C input to soil in response to 611 elevated CO<sub>2</sub> intensifies PIPE and SOM turnover (Scenario 1) (Kuzyakov, 2019; Perveen et al., 2014). 612 Moreover, a recent meta-analysis (Terrer et al., 2021) showed that the effect of elevated CO<sub>2</sub> on SOM 613 stocks was best explained by a negative relationship with plant biomass (Scenario 2): when plant 614 biomass is strongly stimulated by elevated CO<sub>2</sub>, SOM storage declines; conversely, when biomass 615 decreases, SOM storage increases. Although plant-soil interactions play a major role in the response 616 of the PIPE to global change, it is important to note that some factors of global change may act on the 617 PIPE and related services independently of soil-plant interactions. For example, moderate atmospheric 618 N depositions have been shown to decrease the microbial production of oxidative enzymes (and the 619 intensity of PIPE leading to SOM accumulation (Hagedorn et al., 2003; Ramirez et al., 2012; Perveen et 620 al., 2014; Liu et al., 2018).

In sum, we propose that global change can deeply impact PIPE, with consequences ranging from a change in plant production to the progressive decline of ecosystems and their services. The consequences of global change on ecosystem services would mostly depend on the ability of plants to keep driving the PIPE and SOM dynamics in a global change context.

- 625
- 626 8 CONCLUSION AND PERSPECTIVES

627

628 After more than 70 years of research on PE, the way it will respond to climate change and 629 impact the flux of C to the atmosphere is still unclear. Research has been strongly intensified 630 these last ten years but a strong global international coordination is still lacking. PE are generated by multiple mechanisms, but many studies continue to focus on the global flux 631 632 without considering the underlying processes. Various processes have been proposed 633 throughout the literature, following context-dependant nomenclature, thus introducing some 634 confusion in subsequent work. Moreover, while the environmental drivers of these 635 mechanisms are roughly known, their respective output on the C cycle merit to be more 636 deeply studied. We have proposed a classification of the different mechanisms according to 637 their putative impact on the soil C balance between sequestration and mineralization. This 638 classification is based on two factors which have to be taken into account: the putative 639 turnover rate of the primed SOM pool and the putative CUE of the microbial populations 640 respiring the primed C. Future studies have to verify these assumptions as some SOM pools, 641 especially the MAOM, are likely characterised by a wider range of turnover rates than 642 previously thought, depending on the organo-mineral association model and the chemical 643 bonds involved. While wide metagenomic and culturomic studies will continue to increase our 644 knowledge on functional attributes of poorly described microbial populations, the CUE of 645 populations respiring the primed C cannot be extrapolated from the sole identity of present 646 taxa. Actually, many key actors are probably characterized by a wide physiological flexibility, 647 adjusting their CUE and driving different PE generation mechanisms following environmental 648 conditions. Increasing our knowledge on C fluxes driven by the different PE mechanisms will 649 help to introduce the PE into models of SOM dynamics, thus predicting its behavior in 650 response to climate change. Developing *in situ* experiments should also represent a decisive 651 step forward to complete actual knowledge mostly based on incubation experiments. But we 652 are convinced that the PE will not respond directly, but likely through plants, which are the 653 main producers of fresh organic matter generating soil PE. Therefore, the concomitant 654 elevated  $CO_2$ , and plant nutrient requirements, also have to be taken into account.

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- 1196
- 1197 SUPPORTING INFORMATION
- 1198 Appendix S1: History of priming effect exploration.
- 1199 Table S1: List of PE publications from 1973 to April 2021
- 1200 Figure S1: Network of the international scientific community working on the soil priming effect
- Figure S2: Main topics tackled in articles focused on soil priming effect, as deduced from networkanalysis
- 1203

#### 1204 TABLES AND FIGURES

1205TABLE 1List of the main PE generation mechanisms proposed by the literature, with their given1206name, definition, drivers and reference articles. SOM: Soil Organic Matter; FOM: Fresh Organic Matter.1207For each mechanism, the last two columns indicate whether microbial populations assimilating the1208primed carbon are characterized by high or low carbon use efficiency (CUE), assuming that r-strategists1209(or copiotrophs) have high CUE while K-strategists (or oligotrophs) have low CUE, and whether the1210primed SOM pool has a fast, medium or low turnover rate. Generation mechanisms have been colored1211to follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue).

1212

1213TABLE 2List of bacterial and fungal taxonomic groups identified in the literature as associated1214to FOM mineralization and/or to one of the main PE generation mechanisms: negative PE or positive1215PE (supposed to involve high CUE or low CUE actors). PE generation mechanisms have been colored to1216follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue). FOM1217mineralization was not considered in this gradient and was colored in green. In the colored cells, names1218correspond to the specific FOM that generated PE in the different publications.

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1220

1221 FIGURE 1 PE-generation mechanisms occurrence according to (1) the quality of the fresh 1222 organic matter (FOM) in terms of lability vs recalcitrance (L:R) and of carbon to nitrogen ratio (C:N), 1223 and to (2) the availability of mineral nitrogen in the soil solution. Each PE process is evaluated on a C 1224 gain or loss scale depending on the CUE of its actors and the turnover rate of the targeted SOM pool. 1225 Basically, the labile fraction of FOM and available N will favor preferential substrate use (negative PE), 1226 necromass recycling, entombing effect and PE by stoichiometric decomposition (positive PE), which 1227 likely lead to a C gain and an incorporation of N into newly formed biomass. Recalcitrant compounds 1228 of FOM will favor Nutrient mining and Abiotically mediated PE specific to low-CUE populations, likely 1229 leading to a C loss from SOM and a recycling of N from a low turnover pool to a faster one (biomass 1230 and even soil solution). Abiotically mediated PE can also be generated by production of HCO3- H+ 1231 during the intense decomposition of FOM, leading to a loss of C from MAOM by microbial populations 1232 of unknown CUE.

- 1233
- FIGURE 2 MAOM and PE. Conceptual scheme of the abiotically mediated PE of mineral
   associated organic matter
- 1236

FIGURE 3 **Constraints on priming effect models**. The level of detail in modeled mechanisms generally depends on the scale considered with more mechanistic models at small scales and more empirical models at large scales. The objectives also depend on the scale, models developed at small scales generally aim at understanding the priming effect whereas models developed at larger scales aim at quantifying its impacts.

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FIGURE 4 **Global Change effect on PIPE:** The three main scenarios describing the effect of global change on the plant-induced priming effect (PIPE), soil organic matter (SOM) dynamics and four related ecosystem (dis)services (plant production, soil carbon storage, ecosystem carbon storage, nutrient leaching). N = nutrient. The two first scenarios consider that plants maintain their control on SOM dynamics and microbial supply of soluble nutrients while the last scenario considers that plant control is degraded by global change.

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FIGURE 5 Plant control on SOM dynamics: Mechanisms by which plants can modulate soil organic matter (SOM) dynamics in order to adjust the microbial supply of soluble nutrients to plant demand. The plant nutrient demand corresponds to the amount of nutrients needed to convert the carbohydrates produced by photosynthesis into biomass. The nutrient supply corresponds to the release of soluble nutrients by the low-CUE microbial community that is stimulated by plant carbon inputs (plant-induced priming effect, PIPE). Plant C inputs also supply the high-CUE microbial community that builds SOM (storing nutrients and carbon) when plant nutrient demand is low or inexistent. The relative abundance and activity of low-CUE and high-CUE communities is driven by plant uptake of soluble nutrients and carbon inputs (quantity & quality). The numbers indicate the chronology of events.

### Box 1: Shared terminology

**FOM:** Fresh Organic Matter relates to organic matter entering the soil and which will generate a PE on organic matter already present in soil (SOM). It can derive from plants like rhizodeposits (exudates or mucus or dead apical cells) or dead roots, leaves, crop residues or dead animals.

**SOM:** Soil Organic Matter gathers all type of dead organic matter present in the soil before the input of new FOM, from small molecular dissolved compounds to plants residues.

**MAOM:** Mineral Associated Organic Matter designates organic compounds associated to minerals, from small molecules to microbial or plant cell tissues. MAOM is a specific fraction of SOM.

**PE:** In the present review, the Priming Effect is a change in the rate SOM-C mineralization induced by an input of FOM.

**RPE:** The Rhizosphere Priming Effect is the PE generated by live roots and associated rhizosphere organisms when compared to SOM-C mineralisation from rootless soils under the same environmental conditions.

**PIPE:** The plant Induced Priming Effect is the PE induced by whole plants on SOM-C, including RPE but also PE induced by dead roots and aerial parts of plants like litter or crop residues.

# Table 1

PE generation mechanisms			definition	Drivers	References	SOM pool Microbial CUE turnover rate	
SOM decomposition deceleration (negative PE)	real	preferential substrate utilisation	Microbial populations decomposing SOM switch to FOM decomposition.	Labile part of added substrate > 2x microbial biomass Nutrient concentration (soil + substrate) should meet microbial demand	Cheng 1999; Kuzyakov 2000	High and	?
	Tear	Necromass recycling	Microbial populations decomposing SOM switch to the decomposition of the necromass of FOM-decomposers.	Microbial necromass can also be sorbed on minerals. Clays and metals in the soil can compete with microbes for available necromass (Creamer et al. 2019).	Cui et al. 2020	low	
SOM decomposition acceleration (positive PE)	apparent	triggering effect	Acceleration of internal microbial metabolism by trace amounts of substrate with an immediate (several minutes to several hours) increase in the respiratory activity	labile part of added substrate < microbial biomass	Blagodatskaya & Kuzyakov 2008	High and low	Fast
		microbial activation	The N content of the soluble part of the amended substrate will be used to produce first extracellular enzymes. It can also correspond to N-containing root exudates in the rhizosphere.	labile part of added substrate < microbial biomass N rich FOM	Kuzyakov 2002		
		pool substitution	acceleration of the turnover of the whole microbial biomass (several days or weeks)	labile part of added substrate = microbial biomass Blagodatskaya & Kuzyakov 2008			
	real	stoichiometric decomposition	FOM increases biomass and general enzymatic activity, accompanied by domination of r-strategists and increase in SOM decomposition.	FOM complexity with nutrient availability (Plant residues)	Chen et al. 2014	High	
		cometabolism	Assimilation of FOM and SOM by similar populations. FOM brings the energy to decompose less available SOM compounds.	labile part of added substrate superior to microbial biomass; Nutrient availability (substrate and dissolved) slighly inferior to microbial demand	Kuzyakov 2000; Blagodatskaya & Kuzyakov 2008; Yu et al. 2018	High or low	Fast to w medium
		mechanism 1	Enzymes produced by r-strategists in order to decompose FOM may be partially efficient for SOM degradation	FOM complexity with nutrient availability (Plant residues)	Fontaine et al. 2003	Low	
		mechanism 2	K-strategists mineralizing SOM, with slow growth rates, may benefit from FOM polymerised substrates which have a long residence time in soil. Thus K-strategist populations and associated enzyme production increase, causing PE.	labile energy rich substrate with nutrient depletion	Fontaine et al. 2003	Low	Medium
		N-mining	FOM supply increases the biomass and enzymatic activity of K-strategists and increases SOM decomposition.	labile energy rich substrate with N depletion	with N Chen et al. 2014		
		Abiotically mediated	Plant roots exudate organic acids, which desorb labile MOS associated to minerals (MAOM). Liberated compounds will be accessible to microbial decomposition. Fungi and bacteria are also able to produce organic acids or chelatants and could generate such PE	N-limitation	Keiluweight et al. 2015 ; Fang et al. 2018	High and or low ?	Slow

# TABLE 2

phylogenetic Kingdom	affiliation	Phylum	Order	Family	Genus	FOM mineralization	Negative PE	High-CUE PE	Low-CUE PE	References
							Grass residue	Urea, cellulose		Hamer et al. 2009; Potthast et al 2010; Blagodatskaya et al. 2014
		G- (16:1w7c)						Glucose		Derrien et al. 2014
		G- (18:1w7c)						0100000	Glucose	Derrien et al. 2014
		Proteobacteria				Alfalfa residue				Pascault et al. 2013
		Proteobacteria			Unclassified			Wheat residue		Razanamalala et al. 2018a
						Wheat residue		Glucose, wheat residue		Bernard et al. 2012, Razanamalala et al. 2018b; Fang et al. 2018
					Variovorax	Wheat residue			Wheat residue	Bernard et al. 2007; 2009
			Burkholderiales	Comamonadaceae	Acidouorax			Wheat residues	Wheat residue	Bernard et al. 2007
					Aquabacterium			Wheat residues	Wheat residue	Bernard et al. 2007; 2009
		beta-Proteobacteria			Maarilla	Wheet estidue				Bernard et al. 2007; Liu et al.
				Oxalobacreaceae Burkholderiaceae	Massilla	wheat residue				2021
					Janthinobacterium				Wheat residue	Bernard et al. 2009
					Novinerbaspirillum	Chucasa wheat			wheat residue	Liu et al. 2021
					Burkholderia	residue				Arcand et al. 2017; Liu et al. 2021
					Ralstonia				Wheat residue	Liu et al. 2021
					Methylibium				Wheat residue	Bernard et al. 2009
				Pseudomonadaceae Rhodanobacteraceae		Wheat residue		Wheat residues, glucose		Razanamalala et al. 2018a,
		gamma-Proteobacteria	Pseudomonadales Xantomonadales		Pseudomonas	Wheat residue				Bernard et al. 2007
					Dyella				Wheat residue	Liu et al. 2021
						Wheat residue		Wheat residues		Razanamalala et al. 2018a,
						wheat residue		Wheat residues		Maron et al. 2018
	Cromm				cohingocinicalla	Wheat residue			Wheat residue	Bernard et al. 2009
	Grannin		Sphingomonadales	Sphingomonadaceae	Kaistobacter				Wheat residue	Bernard et al. 2007
		alpha-Proteobacteria			sphingomonas	Glucose				Arcand et al. 2017
			Rhizobiales	Methylobacteriaceae		Wheat residue				Bernard et al. 2009
			TTTTEODITIES	Bradyrhizobiaceae	Bradyrhizobium				Wheat residue	Liu et al. 2021
			Hyphomicrobiales	Nitrobacteraceae	Rhodoplanes	Glucose			Wheet residue	Arcand et al. 2017
		-	wicropepsates	Micropepsaceae	Knizomicrobium			Wheat, alfalfa	wheat residue	Bernard et al. 2012: Pascault et
		Bacteroidetes					Biochar	residues, glucose		al. 2013; Arcand et al. 2017
			Chitinophagales	Chitinophagaceae	Flavisolibacter	Wheat residue				liu et al. 2021
										Pascault et al. 2013;
							Tree leaves		rice & wheat residue;	Razanamalala et al. 2018a,b; Maron et al. 2018: Eans et al.
Bacteria		Acidobacteria							Glucose, tree leaves	2018: Yu et al. 2020
			GP2					Wheat residues		Razanamalala et al. 2018a
			GP6					Wheat residues		Razanamalala et al. 2018a
			GP4						Wheat residue	Razanamalala et al. 2018a
			GP1						Wheat residue	Liu et al. 2021 Passault et al. 2012: Merricson et
		Verrucomicrobia				Glucose	Tree leaves	Rice and wheat residue	Wheat residue, tree	al. 2017; Razanamalala et al.
									leaves	2018b; Yu et al. 2020
				Germatimonaceae						Pascault et al. 2013;
		Gemmatimonadetes					Biochar		Wheat residue	Razanamalala et al. 2018b;
			Germatimonales		Germatimonas				Wheat residue	liu et al. 2021
			Gennatinonales	Gennatinonaceae	Gennatinonas			Country of Country of	Whene residue	Razanamalala et al. 2018a.b;
		Planktomycetes			Aquisphaera			Wheat residues	Wheat residue, Glucose	Maron et al. 2018
			Planctomycetales	Isosphaeraceae					Wheat residue	Liu et al. 2021
		Chloroflexi						Rice and wheat residue	Wheat residue	Razanamalala et al. 2018a,b; Maron et al. 2018
	-									Potthast et al. 2010:
			Actinomycetales Micromonosporaless	microccocaceae				Bracken	Cellulose, litter, rice straw and roots	Blagodatskaya et al. 2014; Wang
						-	N		straw and roots	et al. 2014, 2020
										Razanamalala et al. 2018a,b;
						Wheat residue,		Glucose	Wheat residue	Maron et al. 2018; Arcand et al. 2017: Liu et al. 2021: Rereard et
						Glucose			Glucose, wheat residue	al. 2009
										Garcia-Pausas et al. 2011;
										Bernard et al. 2012; Morissey et
									-	al. 2017
		Actinobacteria			Arthrobacter	Glucose Wheat residue				Mau et al. 2015
						Glucose				Morrissey et al. 2017
	Grammi			Streptomycetaceae		Glucose				Arcand et al. 2017
	Grannitt				Streptomyces	Wheat residue				Liu et al. 2021
				micromonosporaceae		Glucose				Morrissey et al. 2017
			Propionibacteriales	Nocardioidaceae		Glucose Wheat residue				Morrissey et al. 2017 Bernard et al. 2009
			Acidimicrobideae	nyphomerobiaceae		Wheat residue			Wheat residue	Bernard et al. 2007
			Gaiellales	Gaiellaceae	Gaiella				Wheat residue	liu et al. 2021
						Wheat residue		Glucose, Alfalfa, rice and wheat residues		Pascault et al. 2013;
										Razanamalala et al. 2018a,b;
										2018; Yu et al. 2020
		Firmicutes	Bacillales	Destille			-			Mau et al. 2015; Arcand et al.
				васшасеае	Bacillus	wheat residue			Glucose	2017; Liu et al. 2021
				Paenibacillaceae Alicyclobacillaceae	Paenibacillus		7		Glucose	Arcand et al. 2017
	-	Upknown			Alicyclobacillus		2		Wheat residue	Liu et al. 2021
fungi	2	Unknown							Wheat residue	Kazanamaiaia et al. 2018a
										namer et al. 2009; Potthast et al. 2010: Garcia-Pausas et al. 2011.
							Tree leaves	linea cellulora brachas	Glucose, cellulose, litter,	Blagodatskaya et al. 2014; Wang
							The leaves	orea, cenulose, bracken	PE	et al. 2014; Shahzad et al. 2018;
										Tian et al. 2019; Fang et al. 2018 Yu et al. 2020
	saprotrophic							Cellulose		Blagodatskava et al. 2014
	saprotrophic	Leothiomycota							Biochar	Yu et al. 2018
		Ascomucota							Wheat residue	Maron et al. 2018
		. Scorrycota	Pezizomycotina	Sordariomycetes					Biochar	Yu et al. 2018
		Basidiomycota	Agaricomunction	Tramellomusctor		Wheat residue			Biochar	Maron et al. 2018
			EUDONING STREET	emenumyuetes					S.Ochar	

# FIGURE 2



### FIGURE 1





Aggregates

# Spatial Scale

Globe



Days

**Time Scale** 

Models with no name (Neill and Gignoux, 2006; Blagodatsky et al., 2010) SYMPHONY (Perveen et al., 2014) SOMKO (Gignoux et al., 2001) Centuries

ORCHIDEE-PRIM (Guenet et al., 2018) MIMICS (Wieder et al., 2013)

# Why to develop a priming model?

Predict the impact on C balance

Increase our Understanding / test assumptions

What are the constraints to develop a priming model?

Parameterization difficulties / Data to evaluate

impacted by other factors

Maximum model complexity / detailed data needed for evaluation

# FIGURE 4



