Exploring the drivers controlling the priming effect and its magnitude in aquatic systems

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25 **Key points:**

- 26 • A meta-analysis was performed to test whether organic matter ‘priming’ occurs in
27 aquatic ecosystems.
- 28 • We show that despite large variability between observations, priming is a
29 generalisable feature of aquatic ecosystems.
- 30 • This variability can be explained by two main factors: How priming is measured
31 and field/laboratory differences.

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33 **Plain Language Summary**

34 In aquatic ecosystems, recently-produced organic matter impacts the activity of
35 decomposers feeding on old, stable organic matter in the same medium. This
36 phenomenon may induce either an increase or a decrease in atmosphere-bound CO₂
37 fluxes, however the drivers controlling this phenomenon remain unclear. Here, we use a
38 literature-based data synthesis to show that in general the addition of freshly-produced
39 organic matter increases the decomposition, and hence the atmospheric CO₂ flux, of
40 older, more stabilized organic matter (i.e., ‘priming’). Compared to previous studies, we
41 found that detection of priming appears to be related to the conditions of measurement
42 (laboratory vs. field) and the proxies used to estimate priming (CO₂, dissolved organic
43 carbon consumption, etc.), suggesting that complex physiological mechanisms control the
44 observed effect on CO₂ fluxes.

45

Abstract

Changes in mineralization rates of stable or persistent organic matter induced by inputs of labile organic matter can alter the organic carbon (C) balance along the terrestrial-aquatic ecosystem continuum. This phenomenon, also known as the priming effect, is well-established in terrestrial ecosystems, but has only recently been explored in the domain of aquatic ecology– with widely contrasting responses of stable carbon to the priming effect reported across the literature. Here, we compiled data from experimental studies on C mineralization in aquatic systems that directly or indirectly tested for the priming effect, and used a meta-analytic approach to investigate the physical and chemical drivers behind the differing outcomes reported across studies. We found that the reported heterogeneity could be explained by two main factors: how the priming effect is measured and whether the study was performed in the laboratory or under field conditions. These findings suggest that how the priming effect is tested and measured has strong implications for its detection and magnitude.

1. Introduction

Both freshwater and marine ecosystems receive and process large amounts of organic matter that are exported from terrestrial and in-stream primary production (1.9 Pg C yr⁻¹, of which 0.9 Pg C yr⁻¹ reaches the continental shelf (Cole et al., 2007)). This organic matter is highly heterogeneous in its resistance to degradation (Jiao et al., 2010), with highly recalcitrant organic matter generally originating from terrestrial vegetation inputs (Amon & Benner, 1996; Thorp & Delong, 2002). More reactive or 'labile' molecules tend to be sourced from in-stream or 'autochthonous' primary production (R.L. Sinsabaugh & Foreman, 2003), although this is also a source of the most persistent organic matter (Kothawala et al., 2014; Kellerman et al., 2015). As such, aquatic systems are sites of intense loading and processing of organic matter (Regnier et al., 2013).

Through a process known as the “*priming effect*”, labile organic matter (LOM) can interact with stable organic matter (SOM), altering the latter's rate of mineralization (Fontaine et al., 2003; Kuzyakov et al., 2000). As such, the metabolic activity of microorganisms can be stimulated or inhibited by labile carbon (C) inputs, respectively referred to as positive or negative priming (Kuzyakov et al., 2000). This process was first described for soils (Löhnis, 1926), with studies demonstrating that it can play a significant role in the soil carbon budget and nutrient cycling (Fontaine et al., 2004; Finzi et al., 2015; Keiluweit et al., 2015; Guenet et al., 2018). In terrestrial ecosystems, positive priming is reported more frequently in laboratory incubations (Kuzyakov et al., 2000), though positive priming has also been demonstrated in field studies (Xiao et al., 2015). Positive priming may therefore under certain conditions reduce soil C storage by enhancing the rate at which soil carbon is metabolised by soil microbiota (Fontaine et al.,

2004). In addition, priming dynamics depend on the interactive effects of abiotic and biotic factors such as substrate availability and accessibility, soil physical-chemical properties, and microbial community structure and activity (Fontaine et al., 2003; Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010). Priming in aquatic ecosystems became a topic of discussion some decades ago (De Haan, 1977), but has recently received renewed interest from freshwater and marine ecosystems researchers (Guenet, et al., 2010a; Bianchi, 2011; Lane et al., 2013). The main mechanisms proposed to explain priming are, firstly, that microbial competition between LOM and SOM specialists can push SOM specialists to feed exclusively on SOM when LOM is added, causing the LOM-specialist populations to grow (Fontaine et al., 2003). Secondly, priming may be caused by nutrient mining, whereby microorganisms increase SOM decomposition in order for them to obtain specific growth-limiting nutrients. Co-metabolism of aquatic microorganisms may be a further explanatory factor (De Haan, 1977). In this study, we defined priming effect in aquatic ecosystems as it was defined in soils, i.e., the modification (acceleration or slowdown) of the mineralization rate of the SOM initially present induced by addition of LOM.

A growing number of studies have shown that priming effects can occur across a wide range of aquatic ecosystems (De Haan, 1977; Shimp & Pfaender, 1985; Carlson et al., 2002; van Nugteren et al., 2009; Farjalla et al., 2009; Danger et al., 2013; Bianchi et al., 2015), and that the rate of the attendant carbon metabolization may be of a similar magnitude to that observed in terrestrial ecosystems (Guenet, et al., 2010a). Concurrently however, these studies also present contrasting and apparently contradicting results, with some suggesting a significant positive priming effect and others a negative or non-

109 existent one (Danger et al., 2013; Franke et al., 2013; Bengtsson et al., 2014; Guenet et
110 al., 2014; Catalán et al., 2015). The drivers of these differences in labile-stable organic
111 matter interactions, as well as the relative importance and magnitude of priming within
112 and across different aquatic ecosystems has remained unclear. Indeed, a recent synthesis
113 on the topic concluded that the priming effect may not be a significant phenomenon in
114 aquatic ecosystems (Bengtsson et al., 2018). However, Bengtsson *et al.* (2018) focused
115 only on primary research studies that explicitly mentioned the term ‘priming’. While this
116 is a valid first approximation, it ignores those studies whose methodology and data
117 collection could have been used to test the priming effect, but which were not originally
118 designed for this purpose. There exists a wealth of prior studies investigating the response
119 of microbial mechanisms to a mix of labile and a native substrates that are appropriate for
120 the inference of the priming effect (Carlson et al., 1998; Farjalla et al., 2009). Therefore,
121 the amount of data available to conduct such meta-analysis may be substantially larger
122 than that considered by Bengtsson *et al.* (2018), meaning their conclusions with respect
123 to the plausibility of aquatic system priming may be premature. Indeed in this vein
124 Bengtsson *et al.* (2018) considered whether much of the observed PE variability might
125 also result from issues in defining the priming effect.

126 In this study, we compiled literature data from experimental studies on C
127 mineralization in aquatic ecosystems that either directly tested the priming effect, or
128 contained data from which we could recalculate the priming effect. We then applied a
129 meta-analytic approach to investigate the study-level characteristics most likely to
130 explain the variation in the occurrence and magnitude of priming in aquatic ecosystems.
131 More specifically we aimed at determining: (1) the overall magnitude of priming across

132 studies; (2) the extent of heterogeneity in results across studies; and (3) the possible
133 biogeochemical and methodological drivers behind the observed differences in priming.
134 We also discuss whether the term ‘priming effect’ should be modified or not as suggested
135 by Bengtsson *et al.* (2018).

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2. Materials and methods

2.1 Literature search, inclusion criteria and data extraction

To find published data directly or indirectly related to the priming effect, we searched the ISI Web of Science for primary research studies using the terms “organic matter AND priming AND aquatic” OR “carbon AND priming AND aquatic” OR “organic matter AND carbon AND aquatic” in the title, abstract, author keywords, or keywords plus. This research was performed on 13th February 2020. We also included the data studied in previous compilations on the PE (Guenet, et al., (2010a); Bengtsson et al., (2014; Blanchet et al., (2016)), resulting in a total of 125 studies considered initially.

In addition, for a study to be included in our meta-analysis it had to meet four criteria: (1) the experimental study was designed to explicitly test the priming effect on C mineralization or had a design through which the priming effect could be calculated *a posteriori* (i.e. the possibility to measure SOM mineralization or microbial activity support by SOM mineralization with or without LOM); (2) the study established a control treatment containing only SOM and an experimental treatment containing both LOM and SOM; (3) the outcome reported by the experiment was a proxy of microbial activity under both priming/no-priming treatments (bacterial growth, bacterial production, bacterial respiration, CO₂ production, DOC (dissolved organic carbon) consumed, extracellular enzyme activity or POC (particulate organic carbon) removed); (4) the study reported the mean, a measure of variability (*e.g.*, standard error, variance or confidence intervals) and the sample size for each of the two treatments. Following these criteria, we included 877 results from experimental treatments from 36 published studies out of the initial 125 in the meta-analysis.

From these, we extracted a number of measures for diagnosing the different outcomes reported across studies (CO₂ production, bacterial production, DOC or POC degradation, enzymatic activities, O₂ consumption), as well as a number of factors detailed below that we hypothesized *a priori* could be drivers of the priming outcome in each study. First, we extracted the statistical means, sample sizes and sample variabilities for each of the two treatments from each experiment in our meta-analysis. We extracted these data directly from the text and tables, or used the software Engauge Digitizer v4.1 in cases where such data was presented in figures. Then, for each study, we recorded from the papers text or tables the several factors that could be drivers for priming. We collected the type of ecosystem studied (four levels: lake, lagoon, river/stream or marine/sea), the experimental venue (two levels: *in situ* or laboratory experiments) and the identity of the priming-inducing LOM (four levels: glucose, algae, diatoms or other (referring to any LOM not in the three previous categories; the category diatoms was created separately from alga level due high number of experiments that used specifically this taxa as priming inductor, in general used diatom detritus as LOM). We also collected the presence or absence of particulate organic carbon (POC; two levels), whether nutrients were added to the medium (four levels: no addition, N addition, P addition, N and P addition), the temperature (Celsius) and the duration of the experiment (in days).

2.2 Vote counting and effect size calculation

We used two approaches to analyze the extent of occurrence and the variation in the magnitude of the priming effect across studies. First, we used the results reported by the authors from each study to code a categorical variable indicating whether the priming

effect occurred or not and, if it occurred, whether it accelerated (positive priming) or slowed down C mineralization (negative priming). Nevertheless, not all the studies used in our analysis were designed to study the PE and thus, this information was sometimes missing. Moreover, in the studies we gathered, the authors do not use a common metric and the comparison between studies is therefore difficult. Thus, in our second approach, we calculated a metric for quantifying the magnitude of priming for each observation in each study and at each time step. We chose the log response ratio as the effect size metric, a measure commonly used in ecological meta-analysis (Rosenberg et al., 2013). This metric quantifies, for each observation in each study, the log of the ratio between the outcome in the experimental treatment (*i.e.*, SOM + LOM) and the control treatment (*i.e.*, SOM only), with positive values indicating that the priming effect accelerated C mineralization, and negative values indicating the opposite. From here on, we refer to this priming magnitude metric as the priming response ratio (PRR) according to

$$PRR = \log (R_{pt}/R_{ct}) \quad (1)$$

Where PRR refers to priming effect in absolute values, R_{pt} to the difference of OM degradation in the priming treatment (SOM + LOM) between beginning and end of experiment, and R_{ct} to the difference of OM degradation in the control treatment (only SOM) between beginning and end of experiment. PRR calculation allowed us compare OC degradation reported in a variety of different units (e.g. DOC removed, C respired, leaf mass loss).

2.3 Statistical analyses

2.3.1 Estimation of the overall priming magnitude

We used a mixed-effects meta-analysis model to determine the overall magnitude of the priming effect and to quantify its heterogeneity across studies, with PRR as the dependent variable and the inclusion of a random intercept term to account for the non-independence of observations coming from the same study following eq. 2:

$$\log(PPR) = \beta_0 + \beta_1 \times x_{i1} + \dots + \beta_j \times x_{ij} + u_i \quad (2)$$

with β_j the fixed effect of j-th variable, x_{ij} being the value of the j-th moderator variable for the i-th study and u_i being the rand effect associated to the i-th study. Several observations lacked an error term, which prevented us from calculating the sampling variance related to each PRR and, therefore, from being able to weight each observation by its precision. We used an unweighted approach which was not qualitatively different from the weighed approach (supporting information). We verified the assumptions of the model by visual inspection of data and residuals. We then extracted the overall priming effect magnitude across studies and its 95% confidence intervals to test the null hypothesis that the size of an effect is homogenous across studies. We also extracted the Q_T and I^2 statistical heterogeneity measures. Q_T and I^2 describe both the percentage of variation across studies due heterogeneity rather than chance (Cochran, (1954); Higgins & Thompson, (2002). Although Q_T is a classical indicator of heterogeneity, it is sensitive to the number of studies, which is not the case with I^2 .

2.3.2 Identification of the explaining factors

We then sought to determine which factors were most likely to explain differences in priming magnitude across studies. To this end, we used the same methods described in 2.3.1 but we fitted eight separate models using each of the seven predictor

variables extracted (type of ecosystem, experimental venue, identity of the priming inductor, POC presence, nutrient addition, temperature and experimental duration) and a predictor variable coding the type of response variable used by authors to characterize the priming effect in each study used in meta-analysis (categorical, seven levels: bacterial growth, bacterial production, bacterial respiration, CO₂ production, DOC degradation, extracellular enzyme activity or POC removed). We included both a linear and a quadratic term for temperature in the model when using this variable as a predictor, given the non-linear effects of temperature in most biological process (Brown et al., 2004). We ran a separate model for each of these predictors, as our main aim was to gain a general understanding of the factors contributing to the variation in priming magnitude, rather than the complex interactions between the predictors. After fitting each of the models, we verified the assumptions of the model by visual inspection of data and residuals, extracted the overall effect size for each level of the non-continuous (i.e. categorical) factors and their 95% confidence intervals, the overall slope of the effect of the continuous factors and, finally, calculated the Q_T and I^2 heterogeneity measures for each model. The model tests whether a predictor is significant by comparing the log (PPR) distribution against 0. If the p-value associated is lower than 0.05 the predictor is considered as significant. Nevertheless, to take into account the risk of inflating the type 1 error when reproducing those analysis, we corrected the p-value using the Holm-Bonferonni method (Holm, 1979). We ran all analysis using R v3.5.1, and fitted the mixed-effects meta-analysis models using the function *rma.mv* available in the package *metafor* (Viechtbauer, 2010). This approach is widely used to perform meta-analysis (Schädel et al., 2016; Senior et al.,

251 2016; Meurer et al., 2018; Chen et al., 2020; Terrer et al., 2021). All the analysis methods
252 are summarized in Table 1.

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3. Results

3.1 Is priming observed in aquatic ecosystems? Estimations using vote-counting approach or mixed-effects meta-analysis model.

Most of the studies analyzed reported an absence of the priming effect (Figure 1). Specifically, this was the case for 65% out the 877 observations included in our analysis, whereas only 27% of the observations were related to a positive and 7% to a negative priming effect. However, the variability in PRR values across these three categories was very high, especially for reports on positive priming effects (Figure 2).

In contrast to the vote counting approach, the mixed-effects meta-analysis model provided support for a positive priming effect across studies (Figure 3, PRR: 0.43; 95% CI: 0.21 to 0.65), indicating that the addition of LOM accelerates microbial activity on SOM by 53.7% on average (95% CI: 23.4% to 91.6%). Yet, this model also revealed that there is a high heterogeneity in observed outcomes across experiments, with 91.4% of the variation in the overall effect size explained by differences between studies (I^2 metric; σ^2_{study} : 0.281).

3.2 Identification of the explaining factors

The mixed-effects meta-analysis model indicated that such heterogeneity could be explained by methodological and environmental differences between studies (Figures 4, 5 and 6). First, we found that the proxy used to estimate the priming effect in each experiment may be a key driver determining whether it can be detected or not. This is because the (positive) priming effect was mostly reported when it was estimated via CO₂ production (0.53 [0.22 to 0.84]) or bacterial growth (PRR [95% CI]: 1.27 [0.40 to 2.13]). We noted that using bacterial production (0.74 [0.20 to 1.28]), extracellular enzyme

activities (0.92 [0.10 to 1.74], tends to detect priming but those variables were not significant after the Holm-Bonferonni correction. Other measures such as bacterial respiration, DOC degradation and POC removal were unlikely to detect the priming effect (Figure 3a). Second, experiments conducted in the laboratory often reported a positive priming effect (0.43 [0.19 to 0.67]), while the same did not occur in experiments performed *in situ* (0.44 [-0.17 to 1.06]) (Figure 4b).

Adding N or P may impact observed priming effect even though the PPR values were generally close. Indeed, only when N and P were simultaneously added to the experiment (0.40 [0.14 to 0.67]) or neither was added (0.45 [0.21 to 0.69]) were effects statistically significant after the Holm-Bonferonni correction (insignificant when N (0.48 [0.12 to 0.83]) or P (0.42 [0.06 to 0.77]) were added in isolation, (Figure 5a)). In addition, the priming effect was not detected when the type of the LOM added was in the form of diatoms (0.43 [-0.11 to 0.97]) or algae (0.41 [-0.02 to 0.83]). A trend was observed for glucose (glucose: 0.36 [0.06 to 0.66]) addition but the effect was not considered significant. Finally, priming was significantly detected with the last categories referring to any LOM not in the three previous categories (other: 0.45 [0.17 to 0.73]) (Figure 5b). POC addition may impact whether priming is detected (0.39 [0.08 to 0.71]) since the priming was not considered significant after POC addition, whereas it was in experiments in which it was excluded (0.48 [0.16 to 0.79]) (Figure 5c).

We found that the priming effect tends to be reduced when increasing experimental duration (intercept, β_0 : 0.59 [0.33 to 0.86]; β_{duration} : -0.06 [-0.14 to -6.14 10^{-4}]). Moreover its magnitude seems affected by the temperature at the time of measurement (Figure 6). More specifically, we found a non-linear relationship between

temperature and the magnitude of the PE, which was absent or weak when experimental temperatures were below 20 °C, but became increasingly positive and strong above it (β_0 : 1.68 [-0.55 to 3.91]; $\beta_{\text{temperature}}$: -0.20 [-0.45 to 0.05]; $\beta_{\text{temperature}^2}$: 0.007 [-4.3 10^{-6} to 0.01]; Figure 6b). Nevertheless, after Holm-Bonferonni correction these effects were not considered significant. Finally, because of non-orthogonality across the levels of both factors or because some treatment combinations were restricted to a single study, we were not able to look at interactions between moderators.

4. Discussion

4.1 The overall priming magnitude.

From the meta-analytic approach employed in this study we observed that, when it occurs, the addition of LOM increased C mineralization rates in aquatic ecosystems, on average, by 53.7%, indicating an overall positive priming effect. However, we note that the variability between and even within studies was quite large. This explains why the vote-counting method provides different results compared to the meta-analysis approach. Indeed the vote-counting approach shows that most of the studies gathered in our database failed to observe priming. Nevertheless, our meta-analysis approach suggests overall positive priming. This apparent contradiction is partly due to the database used. Indeed, for the vote-counting approach, we can only use studies that calculated priming whereas for the meta-analysis we can post calculated priming when all the necessary data were presented in a paper. Thus, the database used for the meta-analysis is larger than the one used for the vote-counting. Moreover, by using the meta-analysis approach we standardized the way priming effect is calculated and thus the statistical power a largely higher than a single study helping identifying some effect (Stewart, 2010). One of the explanations for this large variability might be the diversity of methods used to detect priming, whereby some measurement proxies barely observe priming while others (bacterial growth, CO₂ production) do (Fig.4). Because priming is the result of a number of microbial process at the community level or even at the individual level, measuring the direct effect of LOM addition on bacterial growth may be a more straightforward and less variable means for measuring the priming effect compared to other proxies such as enzymatic activities or C mineralization by mass differences. Otherwise microbial

respiration didn't show efficiency in measured PE, although is the result of enzymatic activity but also on carbon use efficiency, as well as bacterial growth and bacterial production, which is known to be affected by environmental conditions (Manzoni et al., 2012; Sinsabaugh et al., 2013). Moreover, an important fraction of the studies available to perform such meta-analysis do not used labeled organic matter to track the mineralization of SOM and LOM separately and performed a control treatment with SOM only and a SOM+LOM treatment but do not perform a control with only LOM. It is therefore difficult to finely estimate priming since the dynamic of both source of OM cannot be tracked in absence of labeling. This is also a source of variability that may explain the apparent discrepancies between studies.

4.2 Identification of the explaining factors

It is interesting to note that bacterial respiration and CO₂ production give quite different results as priming predictors, even though CO₂ production is largely the result of microbial respiration. This may be related to the fact that the methods used to estimate both fluxes are quite different. Indeed, bacterial respiration is often inferred from O₂ consumption rates measured using variable methods with traditional Winkler method (Winkler, 1888) and modern approaches (Marchand et al., 2009; Del Giorgio et al., 2011) whereas CO₂ production is measured using gas chromatography or by being trapped in NaOH. Another explanation for the discrepancies between CO₂ production and O₂ consumption might be a change in respiratory quotient (moles produced CO₂ per mole consumed O₂) in response to the use of different OM qualities. Results of respiratory quotient are intimately linked to the elemental composition of the respired substrates (Berggren et al., 2012). Priming proxied on bacterial respiration showed higher

variability than results based on CO₂ production. Based on those results, we suggest that to detect priming we should use bacterial growth. On the other hand to diagnose the impact of priming on the C balance, CO₂ production may be the appropriate proxy, being potentially sensitive enough to detect it, whilst bearing in mind that CO₂ production may also result from abiotic processes (Anesio et al., 2005). These suggestions are in line with those of Bengtsson et al., (2018) who suggested to focus on microbial activity to better understand the role of LOM inputs on the ecosystem C cycle. The differences in priming response observed in aquatic ecosystems due to divergent methodologies has not been previously identified in soils, where the priming effect concept was originally defined, because in soil science the methods used to study priming are generally quite comparable. In these, labeled LOM is added to the medium (e.g. Hamer *et al.* 2004; Shahzad *et al.* 2015; Qiao *et al.* 2016) and CO₂ production is measured, and the subsequent use of the carbon isotopes and mass balance equations help to discriminate the source of the produced CO₂. It is possible that by using a single experimental approach, positive priming is more often reported in soils than in the aquatic realm (see Blagodatskaya & Kuzyakov 2008 for review).

It is interesting that nutrient addition in terrestrial ecosystems is often associated with a reduced priming effect due to nutrient mining (Blagodatskaya et al., 2007; Fontaine et al., 2004). However, we observed that adding N and P together give similar results that when nutrients were not added leading in all cases to a positive priming effect. Nevertheless, when only N or P was added the priming observed was not significant. As such, in contrast to what happens in soils, this result suggests that nutrient mining may not be a major driver of priming in aquatic ecosystems (Langley et al., 2009; Chen et al.,

2014). Indeed, in soils organic matter may be stored for millennia (Balesdent et al., 2018) and the stabilization process substantially increases the energetic cost required to obtain nutrients. Thus, when LOM is added to soils it provides enough energy for microbiota to mineralize the nutrients. In aquatic ecosystems, such effect of nutrient seems not to be an important driver (Wologo et al., 2021). Our results therefore suggest that the drivers of priming may be different in terrestrial versus aquatic systems. We also observed that outside of diatom and algae inputs, all types of LOM addition could induce priming but the effect of glucose was not significant after using Holm-Bonferonni correction. It is difficult to understand why priming was significant only for the category 'others' because it represents a large diversity of molecules and not enough data were available to split it up. This should be a future line of inquiry.

4.3 Should we keep calling it priming?

Bengtsson *et al.* (2018) recently published a meta-analysis whose aim was similar to, yet whose methods were different from this study, and showed no significant effect of LOM addition on C mineralization rates (positive priming of 12.6% with a 95% CI ranging from -5.6% to 34.3%). However, Bengtsson *et al.* (2018) selected studies that used mostly bacterial respiration and carbon mineralization measured by mass differences (either DOC or POC) to measure the priming effect, which our results suggest are methods that can hardly ever detect this phenomenon (Fig.4). It is unsurprising that mass-loss methods failed to detect any changes since they are used on relative short-term incubations (few days to few weeks) and, to be detected by classical method, a mass loss must be important enough. As such, this can explain why our work and that of Bengtsson

et al. (2018) arrived at entirely different conclusions. Yet, it is interesting to note that our 95% CI from the estimate of the mixed-effects model falls within the 95% CI of Bengtsson *et al.* (2018). This suggests that both studies are mutually consistent, with the addition that this study pulls apart the drivers of priming heterogeneity. Future studies should take into account this heterogeneity of measurement technique in when designing and reporting experiments relating to the priming effect.

Experimental duration was not a significant driver of aquatic priming after Holm-Bonferonni correction. This result is not coherent with results on the priming effect in soils where long-term effect are often observed (Šantrůčková *et al.* 2004; Luo *et al.* 2011; van Groenigen *et al.* 2014; Guenet *et al.* 2018). Furthermore, it is important to consider that LOM inputs into ecosystems vary seasonally and inter-annually (Giordano *et al.*, 2005; Högberg *et al.*, 2010). This is of particular interest in a global change context where atmospheric CO₂ may induce higher net primary production both in land and aquatic ecosystems (Norby *et al.*, 2005; Borchard & Engel, 2012). As a consequence, we suggest that if the aim of the experiment is to evaluate the impact of priming under changing conditions on the ecosystem functioning or on C balance, long-term experiments have to be performed that replicate variability in the inputs associated to long-term trends. In the future, global temperatures will increase irrespective of differences between anthropogenic emissions scenarios (Anav *et al.*, 2013). We show here that priming tends to be sensitive to temperature, and is positively related to it when incubation temperatures exceed 20°C but this effect was not significant after Holm-Bonferonni correction, the effect of temperature on priming is therefore not clear similarly to results found for the temperature sensitivity of soil priming (Ghee *et al.*,

2013; Z. Luo et al., 2016). This large variability of the results might be due to the use of metabolic proxies (bacterial growth or production) in studies from aquatic ecosystems, which are processes more sensitive to temperature than CO₂ fluxes leading to high variability. However, we are unable to explore this in depth here because we did not look at the interactions between drivers.

Finally, Bengtsson *et al.* (2018) suggested that the term ‘priming effect’ should be changed to “interactive effect among OC pools” to avoid confusion, and to acknowledge the chemical diversity present in OC, instead of continuing to work in terms of 'labile' and 'recalcitrant' OC pools. This is specially appropriate in aquatic systems where intrinsic properties seem to be more relevant than in soils (Kellerman et al., 2015) even though interactions with abiotic and environmental variables such as minerals are now considered as important driver of OC dynamic in aquatic ecosystems (Littlefair et al., 2017; Groeneveld et al., 2020; Kothawala et al., 2020). We agree with this proposition and we even consider that grouping several mechanisms into a general term like *priming* is misleading because the interactive effect observed is the result of more than one mechanisms and the balance between each mechanism explain the intensity of the interactive effect observed. We considered particularly that grouping negative and positive priming under the same “conceptual umbrella” is a source of misunderstanding and confusion. Negative priming is generally a change of substrate by SOM consumers who switch to LOM when enough nutrients are available without a necessary increase in microbial activity. This mechanism is known as preferential substrate utilization hypothesis (Sparling et al., 1982) and is often used to explain negative priming (Cheng, 1999; Guenet, et al., 2010b). Furthermore, positive priming is necessarily a consequence

of an increase in microbial activity, but here again several mechanisms have been proposed to explain priming, adding to the confusion. Priming is therefore a concept grouping together several mechanisms, and we suggest to individually study those mechanisms when possible or at least to measure enough variables to be able to identify the main driving mechanisms (enzymatic activities, nutrient release, microbial community structure and biomass, etc.). What we call priming is therefore not a mechanism, but a pattern; and the mechanisms behind this pattern should be better understood - in particular how the different mechanisms interact with each other.

In conclusion, our study shows that the priming effect may occur in aquatic ecosystems, in contrast to a preceding meta-analysis. The discrepancies between priming effects in the studies included herein result from the methodological and environmental differences between them. Altogether, these findings suggest that how the priming effect is tested and measured by aquatic ecologists has strong implications for its detection, sign and magnitude.

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LFS and BG designed the study. LFS compiled and preprocessed the data. NACM wrote and ran the meta-analysis scripts. All the authors analyzed the results and wrote the paper.

The database used in this study is available at <https://doi.org/10.5281/zenodo.4900670>

REFERENCES

- Amon, R. M. W., & Benner, R. (1996). Bacterial Utilization of Different Size Classes of Dissolved Organic Matter. *Limnology and Oceanography*, 41(1), 41–51.
- Anav, a., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., et al. (2013). Evaluating the Land and Ocean Components of the Global Carbon Cycle in the Cmp5 Earth System Models. *Journal of Climate*, 130401082723008. <https://doi.org/10.1175/JCLI-D-12-00417.1>
- Anesio, A. M., Graneli, W., Aiken, G. R., Kieber, D. J., & Mopper, K. (2005). Effect of humic substance photodegradation on bacterial growth and respiration in lake water. *Applied and Environmental Microbiology*, 71(10), 6267. <https://doi.org/10.1128/AEM.71.10.6267>
- Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., & Hatté, C. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, 23, 1. <https://doi.org/10.1038/s41586-018-0328-3>
- Bengtsson, M. M., Wagner, K., Burns, N. R., Herberg, E. R., Wanek, W., Kaplan, L. a, & Battin, T. J. (2014). No evidence of aquatic priming effects in hyporheic zone microcosms. *Scientific Reports*, 4, 5187. <https://doi.org/10.1038/srep05187>
- Bengtsson, M. M., Attermeyer, K., & Catalán, N. (2018). Interactive effects on organic matter processing from soils to the ocean: are priming effects relevant in aquatic ecosystems? *Hydrobiologia*. <https://doi.org/10.1007/s10750-018-3672-2>
- Berggren, M., Lapierre, J. F., & Del Giorgio, P. A. (2012). Magnitude and regulation of bacterioplankton respiratory quotient across freshwater environmental gradients. *ISME Journal*, 6(5), 984–993. <https://doi.org/10.1038/ismej.2011.157>

498 Bianchi, T. S. (2011). The role of terrestrially derived organic carbon in the coastal
 499 ocean: A changing paradigm and the priming effect. *Proceedings of the National*
 500 *Academy of Sciences*, 108(49), 19473–19481.
 501 <https://doi.org/10.1073/pnas.1017982108>

502 Bianchi, T. S., Thornton, D. C. O., Yvon-Lewis, S. A., King, G. M., Eglinton, T. I.,
 503 Shields, M. R., et al. (2015). Positive Priming of Terrestrially-Derived Dissolved
 504 Organic Matter in a Freshwater Microcosm System. *Geophysical Research Letters*,
 505 42(13). <https://doi.org/10.1002/2015GL064765>

506 Blagodatskaya, E., Blagodatsky, S., Anderson, T. T. H., Y, & Kuzyakov, Y. (2007).
 507 Priming effects in Chernozem induced by glucose and N in relation to microbial
 508 growth strategies. *Applied Soil Ecology*, 37(1–2), 95–105.
 509 <https://doi.org/10.1016/j.apsoil.2007.05.002>

510 Blagodatskaya, E., & Kuzyakov, Y. (2008). Mechanisms of real and apparent priming
 511 effects and their dependence on soil microbial biomass and community structure:
 512 critical review. *Biology and Fertility of Soils*, 45(2), 115–131.
 513 <https://doi.org/10.1007/s00374-008-0334-y>

514 Blanchet, M., Pringault, O., Panagiotopoulos, C., Lefèvre, D., Charrière, B., Ghiglione,
 515 J.-F., et al. (2016). When riverine dissolved organic matter (DOM) meets labile
 516 DOM in coastal waters: changes in bacterial community activity and composition.
 517 *Aquatic Sciences*. <https://doi.org/10.1007/s00027-016-0477-0>

518 Borchard, C., & Engel, a. (2012). Organic matter exudation by *Emiliania huxleyi* under
 519 simulated future ocean conditions. *Biogeosciences*, 9, 3405–3423.
 520 <https://doi.org/10.5194/bg-9-3405-2012>

521 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward
 522 a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789.
 523 <https://doi.org/10.1007/s11064-010-0308-y>

524 Carlson, C., Ducklow, H., Hansell, D., & WO. (1998). Organic carbon partitioning
 525 during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea.
 526 *Limnology And*, 43(3), 375–386. Retrieved from
 527 <http://www.jstor.org/stable/2839087>

528 Carlson, C. A., Giovannoni, S. J., Hansell, D. A., Goldberg, S. J., Parsons, R., Otero, M.
 529 P., et al. (2002). Effect of nutrient amendments on bacterioplankton production,
 530 community structure, and DOC utilization in the northwestern Sargasso Sea. *Aquatic*
 531 *Microbial Ecology*, 30, 19–36.

532 Catalán, N., Kellerman, A. M., Peter, H., Carmona, F., & Tranvik, L. J. (2015). Absence
 533 of a priming effect on dissolved organic carbon degradation in lake water.
 534 *Limnology and Oceanography*, 60(1), 159–168. <https://doi.org/10.1002/lno.10016>

535 Chen, J., Elsgaard, L., van Groenigen, K. J., Olesen, J. E., Liang, Z., Jiang, Y., et al.
 536 (2020). Soil carbon loss with warming: New evidence from carbon-degrading
 537 enzymes. *Global Change Biology*, 26(4), 1944–1952.
 538 <https://doi.org/10.1111/gcb.14986>

539 Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., et al.
 540 (2014). Soil C and N availability determine the priming effect: Microbial N mining
 541 and stoichiometric decomposition theories. *Global Change Biology*, 20(2014),
 542 2356–2367. <https://doi.org/10.1111/gcb.12475>

543 Cheng, W. (1999). Rhizosphere feedbacks in elevated CO₂. *Tree Physiology*, 19(4–5),

544 313–320. Retrieved from
 545 <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Rhizosphere+feed>
 546 [backs+in+elevated+CO+2#0](http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Rhizosphere+feed)

547 Cochran, W. G. (1954). The Combination of Estimates from Different Experiments.
 548 *Biometrics*, 10(1), 101. <https://doi.org/10.2307/3001666>

549 Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G.,
 550 et al. (2007). Plumbing the Global Carbon Cycle: Integrating Inland Waters into the
 551 Terrestrial Carbon Budget. *Ecosystems*, 10(1), 172–185.
 552 <https://doi.org/10.1007/s10021-006-9013-8>

553 Danger, M., Cornut, J., Chauvet, E., Chavez, P., & Elger, A. (2013). Benthic algae
 554 stimulate leaf litter decomposition in detritus-based headwater streams : a case of
 555 aquatic priming effect ? *Ecology*, 94(7), 1604–1613. <https://doi.org/10.1890/12->
 556 0606.1

557 Farjalla, V., Marinho, C., Faria, B., Amado, A., Esteves, F., Bozelli, R., & Girollo, D.
 558 (2009). Synergy of fresh and accumulated organic matter to bacterial growth.
 559 *Microbial Ecology*, 57(4), 657–66. <https://doi.org/10.1007/s00248-008-9466-8>

560 Finzi, A. C. A. C., Abramoff, R. Z. R. Z., Spiller, K. S. K. S., Brzostek, E. R. E. R.,
 561 Darby, B. A. B. A., Kramer, M. A. M. A., & Phillips, R. P. R. P. (2015).
 562 Rhizosphere processes are quantitatively important components of terrestrial carbon
 563 and nutrient cycles. *Global Change Biology*, 21(5), 2082–2094.
 564 <https://doi.org/10.1111/gcb.12816>

565 Fontaine, Sebastien, Bardoux, G., Abbadie, L., & Mariotti, A. (2004). Carbon input to
 566 soil may decrease soil carbon content. *Ecology Letters*, 7(4), 314–320.

567 <https://doi.org/10.1111/j.1461-0248.2004.00579.x>

568 Fontaine, Sébastien, Mariotti, A., & Abbadie, L. (2003). The priming effect of organic
569 matter: a question of microbial competition? *Soil Biology and Biochemistry*, 35(6),
570 837–843. [https://doi.org/10.1016/S0038-0717\(03\)00123-8](https://doi.org/10.1016/S0038-0717(03)00123-8)

571 Franke, D., Bonnell, E. J., & Ziegler, S. E. (2013). Mineralisation of dissolved organic
572 matter by heterotrophic stream biofilm communities in a large boreal catchment.
573 *Freshwater Biology*, 58(10), 2007–2026. <https://doi.org/10.1111/fwb.12187>

574 Ghee, C., Neilson, R., Hallett, P. D., Robinson, D., & Paterson, E. (2013). Priming of soil
575 organic matter mineralisation is intrinsically insensitive to temperature. *Soil Biology
576 and Biochemistry*, 66, 20–28. <https://doi.org/10.1016/j.soilbio.2013.06.020>

577 Giordano, M., Beardall, J., & Raven, J. a. (2005). CO₂ concentrating mechanisms in
578 algae: mechanisms, environmental modulation, and evolution. *Annual Review of
579 Plant Biology*, 56, 99–131.
580 <https://doi.org/10.1146/annurev.arplant.56.032604.144052>

581 Del Giorgio, P. A., Condon, R., Bouvier, T., Longnecker, K., Bouvier, C., Sherr, E., &
582 Gasol, J. M. (2011). Coherent patterns in bacterial growth, growth efficiency, and
583 leucine metabolism along a northeastern Pacific inshore-offshore transect.
584 *Limnology and Oceanography*, 56(1), 1–16.
585 <https://doi.org/10.4319/lo.2011.56.1.0001>

586 Groeneveld, M., Catalán, N., Attermeyer, K., Hawkes, J., Einarsdóttir, K., Kothawala, D.,
587 et al. (2020). Selective Adsorption of Terrestrial Dissolved Organic Matter to
588 Inorganic Surfaces Along a Boreal Inland Water Continuum. *Journal of
589 Geophysical Research: Biogeosciences*, 125(3), 1–22.

590 <https://doi.org/10.1029/2019JG005236>

591 van Groenigen, K. J., Qi, X., Osenberg, C. W., Luo, Y., & Hungate, B. A. (2014). Faster
 592 decomposition under increased atmospheric CO₂ limits soil carbon storage. *Science*
 593 (*New York, N.Y.*), 344(6183), 508–9. <https://doi.org/10.1126/science.1249534>

594 Guenet, B., Leloup, J., Raynaud, X., Bardoux, G., & Abbadie, L. (2010). Negative
 595 priming effect on mineralization in a soil free of vegetation for 80 years. *European*
 596 *Journal of Soil Science*, 61(3), 384–391. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2389.2010.01234.x)
 597 2389.2010.01234.x

598 Guenet, Bertrand, Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect:
 599 bridging the gap between terrestrial and aquatic ecology. *Ecology*, 91(10), 2850–
 600 2861. Retrieved from <http://www.esajournals.org/doi/abs/10.1890/09-1968.1>

601 Guenet, Bertrand, Danger, M., Harraut, L., Allard, B., Jauset-Alcala, M., Bardoux, G., et
 602 al. (2014). Fast mineralization of land-born C in inland waters: First experimental
 603 evidences of aquatic priming effect. *Hydrobiologia*, 721(1), 35–44.
 604 <https://doi.org/10.1007/s10750-013-1635-1>

605 Guenet, Bertrand, Camino-Serrano, M., Ciais, P., Tifafi, M., Maignan, F., Soong, J. L., &
 606 Janssens, I. A. (2018). Impact of priming on global soil carbon stocks. *Global*
 607 *Change Biology*, 24(5), 1873–1883. <https://doi.org/10.1111/gcb.14069>

608 De Haan, H. (1977). Effects of benzoate on microbial decomposition of fulvi acids in
 609 Tjeukemeer (The Netherlands). *Limnology and Oceanography*, 22(January), 38–44.

610 Hamer, U., Marschner, B., Brodowski, S., & Amelung, W. (2004). Interactive priming of
 611 black carbon and glucose mineralisation. *Organic Geochemistry*, 35(7), 823–830.
 612 <https://doi.org/10.1016/j.orggeochem.2004.03.003>

613 Higgins, J. P. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-
 614 analysis. *Statistics in Medicine*, 21(11), 1539–1558.
 615 <https://doi.org/10.1002/sim.1186>

616 Högberg, M. N., Briones, M. J. I., Keel, S. G., Metcalfe, D. B., Campbell, C., Midwood,
 617 A. J., et al. (2010). Quantification of effects of season and nitrogen supply on tree
 618 below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a
 619 boreal pine forest. *The New Phytologist*, 187(2), 485–93.
 620 <https://doi.org/10.1111/j.1469-8137.2010.03274.x>

621 Holm, S. (1979). A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian*
 622 *Journal of Statistics*, 6(2), 65–70. <https://doi.org/10.2307/4615733>

623 Jiao, N., Herndl, G. J., Hansell, D. a, Benner, R., Kattner, G., Wilhelm, S. W., et al.
 624 (2010). Microbial production of recalcitrant dissolved organic matter: long-term
 625 carbon storage in the global ocean. *Nature Reviews. Microbiology*, 8(8), 593–9.
 626 <https://doi.org/10.1038/nrmicro2386>

627 Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., & Kleber, M.
 628 (2015). Mineral protection of soil carbon counteracted by root exudates. *Nature*
 629 *Climate Change*, 5(March 2015), 588–595. <https://doi.org/10.1038/nclimate2580>

630 Kellerman, A. M., Kothawala, D. N., Dittmar, T., & Tranvik, L. J. (2015). Persistence of
 631 dissolved organic matter in lakes related to its molecular characteristics. *Nature*
 632 *Geoscience*, 8(6), 454–457. <https://doi.org/10.1038/NGEO2440>

633 Kothawala, D. N., Stedmon, C. A., Müller, R. A., Weyhenmeyer, G. A., Köhler, S. J., &
 634 Tranvik, L. J. (2014). Controls of dissolved organic matter quality: Evidence from a
 635 large-scale boreal lake survey. *Global Change Biology*, 20(4), 1101–1114.

<https://doi.org/10.1111/gcb.12488>
 Kothawala, D. N., Kellerman, A. M., Catalán, N., & Tranvik, L. J. (2020). Organic
 Matter Degradation across Ecosystem Boundaries: The Need for a Unified
 Conceptualization. *Trends in Ecology and Evolution*, 1–10.
<https://doi.org/10.1016/j.tree.2020.10.006>
 Kuzyakov, Y, Friedel, J. K., & Stahr, K. (2000). Review of mechanisms and
 quantification of priming effects. *Soil Biology and Biochemistry*, 32(11–12), 1485–
 1498. [https://doi.org/10.1016/S0038-0717\(00\)00084-5](https://doi.org/10.1016/S0038-0717(00)00084-5)
 Kuzyakov, Yakov. (2010). Priming effects: Interactions between living and dead organic
 matter. *Soil Biology and Biochemistry*, 42(9), 1363–1371.
<https://doi.org/10.1016/j.soilbio.2010.04.003>
 Lane, C. S., Lyon, D. R., & Ziegler, S. E. (2013). Cycling of two carbon substrates of
 contrasting lability by heterotrophic biofilms across a nutrient gradient of headwater
 streams. *Aquatic Sciences*, 75(2), 235–250. [https://doi.org/10.1007/s00027-012-](https://doi.org/10.1007/s00027-012-0269-0)
 0269-0
 Langley, J., McKinley, D., Wolf, A., Hungate, B., Drake, B., & Megonigal, J. (2009).
 Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed
 to elevated CO₂. *Soil Biology and Biochemistry*, 41(1), 54–60.
<https://doi.org/10.1016/j.soilbio.2008.09.016>
 Littlefair, C. A., Tank, S. E., & Kokelj, S. V. (2017). Retrogressive thaw slumps temper
 dissolved organic carbon delivery to streams of the Peel Plateau, NWT, Canada.
Biogeosciences, 14(23), 5487–5505. <https://doi.org/10.5194/bg-14-5487-2017>
 Löhnis, F. (1926). Nitrogen availability of green manures. *Soil Science*, 22, 253–290.

659 Luo, Y., Durenkamp, M., De Nobili, M., Lin, Q., & Brookes, P. C. (2011). Short term
660 soil priming effects and the mineralisation of biochar following its incorporation to
661 soils of different pH. *Soil Biology and Biochemistry*, 43(11), 2304–2314.
662 <https://doi.org/10.1016/j.soilbio.2011.07.020>

663 Luo, Z., Wang, E., & Sun, O. J. (2016). A meta-analysis of the temporal dynamics of
664 priming soil carbon decomposition by fresh carbon inputs across ecosystems. *Soil*
665 *Biology and Biochemistry*, 101(2016), 96–103.
666 <https://doi.org/10.1016/j.soilbio.2016.07.011>

667 Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental
668 and stoichiometric controls on microbial carbon-use efficiency in soils. *New*
669 *Phytologist*, 196(1), 79–91. <https://doi.org/10.1111/j.1469-8137.2012.04225.x>

670 Marchand, D., Prairie, Y. T., & del Giorgio, P. A. (2009). Linking forest fires to lake
671 metabolism and carbon dioxide emissions in the boreal region of Northern Québec.
672 *Global Change Biology*, 15(12), 2861–2873. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2009.01979.x)
673 [2486.2009.01979.x](https://doi.org/10.1111/j.1365-2486.2009.01979.x)

674 Meurer, K. H. E., Haddaway, N. R., Bolinder, M. A., & Kätterer, T. (2018). Tillage
675 intensity affects total SOC stocks in boreo-temperate regions only in the topsoil—A
676 systematic review using an ESM approach. *Earth-Science Reviews*, 177(October),
677 613–622. <https://doi.org/10.1016/j.earscirev.2017.12.015>

678 Norby, R. J., Delucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., et al.
679 (2005). Forest response to elevated CO₂ is conserved across a broad range of
680 productivity. *Proceedings of the National Academy of Sciences of the United States*
681 *of America*, 102(50), 18052–6. <https://doi.org/10.1073/pnas.0509478102>

- van Nugteren, P., Moodley, L., Brummer, G.-J. G.-J., Heip, C. C. H. R., Herman, P. P. M. J., Middelburg, J. J. J., et al. (2009). Seafloor ecosystem functioning: the importance of organic matter priming. *Marine Biology*, 156(11), 2277–2287.
<https://doi.org/10.1007/s00227-009-1255-5>
- Qiao, N., Xu, X., Hu, Y., Blagodatskaya, E., Liu, Y., Schaefer, D., & Kuzyakov, Y. (2016). Carbon and nitrogen additions induce distinct priming effects along an organic-matter decay continuum. *Scientific Reports*, 6(JANUARY), 19865.
<https://doi.org/10.1038/srep19865>
- Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F. T., Gruber, N., Janssens, I. a., et al. (2013). Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nature Geoscience*, 6(8), 597–607. <https://doi.org/10.1038/ngeo1830>
- Rosenberg, M. S., Rothstein, H. S., & Gurevitch, J. (2013). Effect sizes: conventional choices and calculations. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 61–71). Princeton: Princeton University Press.
- Šantrůčková, H., Pícek, T., Tykva, R., Šimek, M., & Pavlů, B. (2004). Short-term partitioning of ¹⁴C-[U]-glucose in the soil microbial pool under varied aeration status. *Biology and Fertility of Soils*, 40(6), 386–392.
<https://doi.org/10.1007/s00374-004-0790-y>
- Schädel, C., Bader, M. K. F., Schuur, E. A. G., Biasi, C., Bracho, R., Capek, P., et al. (2016). Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils. *Nature Climate Change*, 6(10), 950–953.
<https://doi.org/10.1038/nclimate3054>

705 Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. A., &
706 Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses:
707 Its magnitude and implications. *Ecology*, 97(12), 3293–3299.
708 <https://doi.org/10.1002/ecy.1591>

709 Shahzad, T., Chenu, C., Genet, P., Barot, S., Perveen, N., Mougin, C., & Fontaine, S.
710 (2015). Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions
711 to the rhizosphere priming effect induced by grassland species. *Soil Biology and*
712 *Biochemistry*, 80, 146–155. <https://doi.org/10.1016/j.soilbio.2014.09.023>

713 Shimp, R. J., & Pfaender, F. K. (1985). Influence of easily degradable naturally occurring
714 carbon substrates on biodegradation of monosubstituted phenols by aquatic bacteria.
715 *Applied and Environmental Microbiology*, 49(2), 394–401.

716 Sinsabaugh, R.L., & Foreman, C. M. (2003). Integrating Dissolved Organic Matter
717 Metabolism and Microbial Diversity. In *Aquatic Ecosystems* (pp. 425–454). Elsevier.
718 <https://doi.org/10.1016/B978-012256371-3/50019-6>

719 Sinsabaugh, Robert L, Manzoni, S., Moorhead, D. L., & Richter, A. (2013). Carbon use
720 efficiency of microbial communities: stoichiometry, methodology and modelling.
721 *Ecology Letters*, 16(7), 930–939. <https://doi.org/10.1111/ele.12113>

722 Sparling, G. P., Cheshire, M. V., & Mundie, C. M. (1982). Effect of barley plants on the
723 decomposition of ¹⁴C-labelled soil organic matter. *Journal of Soil Science*, 33(1),
724 89–100. <https://doi.org/10.1111/j.1365-2389.1982.tb01750.x>

725 Stewart, G. (2010). Meta-analysis in applied ecology. *Biology Letters*, 6(1), 78–81.
726 <https://doi.org/10.1098/rsbl.2009.0546>

727 Terrer, C., Phillips, R., Hungate, B., Rosende, J., Pett-Ridge, J., Craig, M., et al. (2021).

- A trade-off between plant and soil carbon storage under elevated CO₂. *Nature*,
(March).
- Thorp, J. H., & Delong, M. D. (2002). Dominance of autochthonous autotrophic carbon
in food webs of heterotrophic rivers. *Oikos*, 96(3), 543–550.
<https://doi.org/10.1034/j.1600-0706.2002.960315.x>
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package.
Journal of Statistical Software, 36(3), 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Ward, N. D., Bianchi, T. S., Sawakuchi, H. O., Gagne-maynard, W., Cunha, A. C., Brito,
D. C., et al. (2016). Effects along the lower Amazon River. *Journal of Geophysical
Research: Biogeosciences*, 1522–1539.
<https://doi.org/10.1002/2016JG003342>.Received
- Winkler, L. W. (1888). Die Bestimmung des im Wasser gelösten Sauerstoffes. *Berichte
Der Deutschen Chemischen Gesellschaft*, 21(2), 2843–2854.
<https://doi.org/10.1002/cber.188802102122>
- Wologo, E., Shakil, S., Zolkos, S., Textor, S., Ewing, S., Klassen, J., et al. (2021). Stream
Dissolved Organic Matter in Permafrost Regions Shows Surprising Compositional
Similarities but Negative Priming and Nutrient Effects. *Global Biogeochemical
Cycles*, 35(1), 1–25. <https://doi.org/10.1029/2020GB006719>
- Xiao, C., Guenet, B., Zhou, Y., Su, J., & Janssens, I. a. (2015). Priming of soil organic
matter decomposition scales linearly with microbial biomass response to litter input
in steppe vegetation. *Oikos*, (124), 649–657. <https://doi.org/10.1111/oik.01728>

Figures legends

Figure 1 - Number of observations across all studies included in our meta-analysis reporting positive, negative and no priming effects. The coding of a given observation in one of these categories was based on the results reported for that experiment in each published paper, which compared SOM degradation between a control containing only stable organic matter and a treatment containing both stable and labile organic matter.

Figure 2 – Boxplots showing the distribution of Priming Response Ratios (PRR) across observations from studies reporting positive, negative and no priming effects. A positive PRR indicates that the addition of labile organic matter accelerated the decomposition of the stable organic matter, while negative values indicate the opposite.

Figure 3 – Forest plot of the different studies used to estimate the priming response ratio. Results are log-transformed (mean [95%CI]). A positive PRR indicates that the addition of labile organic matter accelerated the decomposition of the stable organic matter, while negative values indicate the opposite.

Figure 4 – Variation in overall effect sizes of PRR estimated according to (a) how the priming effect is quantified and (b) the experimental venue used to test the priming effect. A positive PRR indicates that the addition of labile organic matter accelerated the decomposition of the stable organic matter, while negative values indicate the opposite. Filled black circles represent levels of the categorical variables that are significantly

different from zero after Holm-Bonferonni correction and, therefore, provide support for the occurrence of priming effect. Filled gray circles represent levels of the categorical variables with confidence-intervals that do not overlap zero but are not significant after Holm-Bonferonni correction. White circles represent levels of the categorical variables with confidence-intervals that overlap zero. Numbers above each category represent the number of observations used in statistical analyses. Vertical bars represent the 95% confidence intervals for each effect size estimate.

Figure 5 – Variation in overall effect sizes of PRR estimated according to (a) whether nutrients were added in the experiment and, if so, which nutrient, (b) the type of labile organic matter (LOM) added in the experimental treatment (labile + stable organic matter) and (c) whether particulate organic matter (POC) was also added to in the experiment. A positive PRR indicates that the addition of labile organic matter accelerated the decomposition of the recalcitrant organic matter, while negative values indicate the opposite. Filled black circles represent levels of the categorical variables that are significantly different from zero after Holm-Bonferonni correction and, therefore, provide support for the occurrence of priming effect. Filled gray circles represent levels of the categorical variables with confidence-intervals that do not overlap zero but are not significant after Holm-Bonferonni correction. White circles represent levels of the categorical variables with confidence-intervals that overlap zero . Numbers above each category represent the number of observations used in statistical analyses. Vertical bars represent the 95% confidence intervals for each effect size estimate.

Figure 6 – Variation in the PRR according to (a) the duration of the experiment and (b) the temperature at the time of the experiment. A positive PRR indicates that the addition of labile organic matter accelerated the decomposition of the stable organic matter, while negative values indicate the opposite. The solid line represents the predicted relationships between PRR and each predictor variable according to a mixed-effects meta-analysis model, and the dashed lines represent its 95% confidence intervals.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

1 Table 1: Summary of the methods used to analyse the database

Objectives	Method use
Estimation of the overall occurrence of priming	Vote-counting approach
Estimation of the overall occurrence and magnitude of priming	Unweighted mixed-effects meta-analysis model
Identification of the explaining factors	Unweighted mixed-effects meta-analysis model with p-value corrected using the Holm-Bonferonni method

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