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

3

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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.

32

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

46

47

48 **Abstract**

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

62

63 **1. Introduction**

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

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

86 2004). In addition, priming dynamics depend on the interactive effects of abiotic and
87 biotic factors such as substrate availability and accessibility, soil physical-chemical
88 properties, and microbial community structure and activity (Fontaine et al., 2003;
89 Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010). Priming in aquatic ecosystems
90 became a topic of discussion some decades ago (De Haan, 1977), but has recently
91 received renewed interest from freshwater and marine ecosystems researchers (Guenet, et
92 al., 2010a; Bianchi, 2011; Lane et al., 2013). The main mechanisms proposed to explain
93 priming are, firstly, that microbial competition between LOM and SOM specialists can
94 push SOM specialists to feed exclusively on SOM when LOM is added, causing the
95 LOM-specialist populations to grow (Fontaine et al., 2003). Secondly, priming may be
96 caused by nutrient mining, whereby microorganisms increase SOM decomposition in
97 order for them to obtain specific growth-limiting nutrients. Co-metabolism of aquatic
98 microorganisms may be a further explanatory factor (De Haan, 1977). In this study, we
99 defined priming effect in aquatic ecosystems as it was defined in soils, i.e., the
100 modification (acceleration or slowdown) of the mineralization rate of the SOM initially
101 present induced by addition of LOM.

102 A growing number of studies have shown that priming effects can occur across a
103 wide range of aquatic ecosystems (De Haan, 1977; Shimp & Pfaender, 1985; Carlson et
104 al., 2002; van Nugteren et al., 2009; Farjalla et al., 2009; Danger et al., 2013; Bianchi et
105 al., 2015), and that the rate of the attendant carbon metabolization may be of a similar
106 magnitude to that observed in terrestrial ecosystems (Guenet, et al., 2010a). Concurrently
107 however, these studies also present contrasting and apparently contradicting results, with
108 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).

136

137 **2. Materials and methods**

138 **2.1 Literature search, inclusion criteria and data extraction**

139 To find published data directly or indirectly related to the priming effect, we
140 searched the ISI Web of Science for primary research studies using the terms “organic
141 matter AND priming AND aquatic” OR “carbon AND priming AND aquatic” OR
142 “organic matter AND carbon AND aquatic” in the title, abstract, author keywords, or
143 keywords plus. This research was performed on 13th February 2020. We also included the
144 data studied in previous compilations on the PE (Guenet, et al., (2010a); Bengtsson et al.,
145 (2014; Blanchet et al., (2016)), resulting in a total of 125 studies considered initially.

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

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

178

179 **2.2 Vote counting and effect size calculation**

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

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

$$196 \quad \text{PRR} = \log (R_{pt}/R_{ct}) \quad (1)$$

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

203

204 **2.3 Statistical analyses**

205 **2.3.1 Estimation of the overall priming magnitude**

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

$$210 \log(PPR) = \beta_0 + \beta_1 \times x_{i1} + \dots + \beta_j \times x_{ij} + u_i \quad (2)$$

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

224

225 **2.3.2 Identification of the explaining factors**

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

229 variables extracted (type of ecosystem, experimental venue, identity of the priming
230 inductor, POC presence, nutrient addition, temperature and experimental duration) and a
231 predictor variable coding the type of response variable used by authors to characterize the
232 priming effect in each study used in meta-analysis (categorical, seven levels: bacterial
233 growth, bacterial production, bacterial respiration, CO₂ production, DOC degradation,
234 extracellular enzyme activity or POC removed). We included both a linear and a
235 quadratic term for temperature in the model when using this variable as a predictor, given
236 the non-linear effects of temperature in most biological process (Brown et al., 2004). We
237 ran a separate model for each of these predictors, as our main aim was to gain a general
238 understanding of the factors contributing to the variation in priming magnitude, rather
239 than the complex interactions between the predictors. After fitting each of the models, we
240 verified the assumptions of the model by visual inspection of data and residuals, extracted
241 the overall effect size for each level of the non-continuous (i.e. categorical) factors and
242 their 95% confidence intervals, the overall slope of the effect of the continuous factors
243 and, finally, calculated the Q_T and I^2 heterogeneity measures for each model. The model
244 tests whether a predictor is significant by comparing the log (PPR) distribution against 0.
245 If the p-value associated is lower than 0.05 the predictor is considered as significant.
246 Nevertheless, to take into account the risk of inflating the type 1 error when reproducing
247 those analysis, we corrected the p-value using the Holm-Bonferonni method (Holm,
248 1979). We ran all analysis using R v3.5.1, and fitted the mixed-effects meta-analysis
249 models using the function *rma.mv* available in the package *metafor* (Viechtbauer, 2010).
250 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.

253

254 **3. Results**

255 **3.1 Is priming observed in aquatic ecosystems? Estimations using vote-**
256 **counting approach or mixed-effects meta-analysis model.**

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

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

269 **3.2 Identification of the explaining factors**

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

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

283 Adding N or P may impact observed priming effect even though the PPR values
284 were generally close. Indeed, only when N and P were simultaneously added to the
285 experiment (0.40 [0.14 to 0.67]) or neither was added (0.45 [0.21 to 0.69]) were effects
286 statistically significant after the Holm-Bonferonni correction (insignificant when N (0.48
287 [0.12 to 0.83]) or P (0.42 [0.06 to 0.77]) were added in isolation, (Figure 5a)). In addition,
288 the priming effect was not detected when the type of the LOM added was in the form of
289 diatoms (0.43 [-0.11 to 0.97]) or algae (0.41 [-0.02 to 0.83]). A trend was observed for
290 glucose (glucose: 0.36 [0.06 to 0.66]) addition but the effect was not considered
291 significant. Finally, priming was significantly detected with the last categories referring
292 to any LOM not in the three previous categories (other: 0.45 [0.17 to 0.73]) (Figure 5b).
293 POC addition may impact whether priming is detected (0.39 [0.08 to 0.71]) since the
294 priming was not considered significant after POC addition, whereas it was in experiments
295 in which it was excluded (0.48 [0.16 to 0.79]) (Figure 5c).

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

300 temperature and the magnitude of the PE, which was absent or weak when experimental
301 temperatures were below 20 °C, but became increasingly positive and strong above it (β_0 :
302 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];
303 Figure 6b). Nevertheless, after Holm-Bonferonni correction these effects were not
304 considered significant. Finally, because of non-orthogonality across the levels of both
305 factors or because some treatment combinations were restricted to a single study, we
306 were not able to look at interactions between moderators.
307

308 **4. Discussion**

309 **4.1 The overall priming magnitude.**

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

331 respiration didn't show efficiency in measured PE, although is the result of enzymatic
332 activity but also on carbon use efficiency, as well as bacterial growth and bacterial
333 production, which is known to be affected by environmental conditions (Manzoni et al.,
334 2012; Sinsabaugh et al., 2013). Moreover, an important fraction of the studies available
335 to perform such meta-analysis do not used labeled organic matter to track the
336 mineralization of SOM and LOM separately and performed a control treatment with
337 SOM only and a SOM+LOM treatment but do not perform a control with only LOM. It is
338 therefore difficult to finely estimate priming since the dynamic of both source of OM
339 cannot be tracked in absence of labeling. This is also a source of variability that may
340 explain the apparent discrepancies between studies.

341 **4.2 Identification of the explaining factors**

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

354 variability than results based on CO₂ production. Based on those results, we suggest that
355 to detect priming we should use bacterial growth. On the other hand to diagnose the
356 impact of priming on the C balance, CO₂ production may be the appropriate proxy, being
357 potentially sensitive enough to detect it, whilst bearing in mind that CO₂ production may
358 also result from abiotic processes (Anesio et al., 2005). These suggestions are in line with
359 those of Bengtsson et al., (2018) who suggested to focus on microbial activity to better
360 understand the role of LOM inputs on the ecosystem C cycle. The differences in priming
361 response observed in aquatic ecosystems due to divergent methodologies has not been
362 previously identified in soils, where the priming effect concept was originally defined,
363 because in soil science the methods used to study priming are generally quite comparable.
364 In these, labeled LOM is added to the medium (e.g. Hamer *et al.* 2004; Shahzad *et al.*
365 2015; Qiao *et al.* 2016) and CO₂ production is measured, and the subsequent the use of
366 the carbon isotopes and mass balance equations help to discriminate the source of the
367 produced CO₂. It is possible that by using a single experimental approach, positive
368 priming is more often reported in soils than in the aquatic realm (see Blagodatskaya &
369 Kuzyakov 2008 for review).

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

377 2014). Indeed, in soils organic matter may be stored for millennia (Balesdent et al., 2018)
378 and the stabilization process substantially increases the energetic cost required to obtain
379 nutrients. Thus, when LOM is added to soils it provides enough energy for microbiota to
380 mineralize the nutrients. In aquatic ecosystems, such effect of nutrient seems not to be an
381 important driver (Wologo et al., 2021). Our results therefore suggest that the drivers of
382 priming may be different in terrestrial versus aquatic systems. We also observed that
383 outside of diatom and algae inputs, all types of LOM addition could induce priming but
384 the effect of glucose was not significant after using Holm-Bonferonni correction. It is
385 difficult to understand why priming was significant only for the category 'others' because
386 it represents a large diversity of molecules and not enough data were available to split it
387 up. This should be a future line of inquiry.

388

389 **4.3 Should we keep calling it priming?**

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

400 *et al.* (2018) arrived at entirely different conclusions. Yet, it is interesting to note that our
401 95% CI from the estimate of the mixed-effects model falls within the 95% CI of
402 Bengtsson *et al.* (2018). This suggests that both studies are mutually consistent, with the
403 addition that this study pulls apart the drivers of priming heterogeneity. Future studies
404 should take into account this heterogeneity of measurement technique in when designing
405 and reporting experiments relating to the priming effect.

406 Experimental duration was not a significant driver of aquatic priming after Holm-
407 Bonferonni correction. This result is not coherent with results on the priming effect in
408 soils where long-term effect are often observed (Šantrůčková *et al.* 2004; Luo *et al.* 2011;
409 van Groenigen *et al.* 2014; Guenet *et al.* 2018). Furthermore, it is important to consider
410 that LOM inputs into ecosystems vary seasonally and inter-annually (Giordano *et al.*,
411 2005; Högberg *et al.*, 2010). This is of particular interest in a global change context
412 where atmospheric CO₂ may induce higher net primary production both in land and
413 aquatic ecosystems (Norby *et al.*, 2005; Borchard & Engel, 2012). As a consequence, we
414 suggest that if the aim of the experiment is to evaluate the impact of priming under
415 changing conditions on the ecosystem functioning or on C balance, long-term
416 experiments have to be performed that replicate variability in the inputs associated to
417 long-term trends. In the future, global temperatures will increase irrespective of
418 differences between anthropogenic emissions scenarios (Anav *et al.*, 2013). We show
419 here that priming tends to be sensitive to temperature, and is positively related to it when
420 incubation temperatures exceed 20°C but this effect was not significant after Holm-
421 Bonferonni correction, the effect of temperature on priming is therefore not clear
422 similarly to results found for the temperature sensitivity of soil priming (Ghee *et al.*,

423 2013; Z. Luo et al., 2016). This large variability of the results might be due to the use of
424 metabolic proxies (bacterial growth or production) in studies from aquatic ecosystems,
425 which are processes more sensitive to temperature than CO₂ fluxes leading to high
426 variability. However, we are unable to explore this in depth here because we did not look
427 at the interactions between drivers.

428 Finally, Bengtsson *et al.* (2018) suggested that the term ‘priming effect’ should be
429 changed to “interactive effect among OC pools” to avoid confusion, and to acknowledge
430 the chemical diversity present in OC, instead of continuing to work in terms of 'labile'
431 and 'recalcitrant' OC pools. This is specially appropriate in aquatic systems where
432 intrinsic properties seem to be more relevant than in soils (Kellerman et al., 2015) even
433 though interactions with abiotic and environmental variables such as minerals are now
434 considered as important driver of OC dynamic in aquatic ecosystems (Littlefair et al.,
435 2017; Groeneveld et al., 2020; Kothawala et al., 2020). We agree with this proposition
436 and we even consider that grouping several mechanisms into a general term like *priming*
437 is misleading because the interactive effect observed is the result of more than one
438 mechanisms and the balance between each mechanism explain the intensity of the
439 interactive effect observed. We considered particularly that grouping negative and
440 positive priming under the same “conceptual umbrella” is a source of misunderstanding
441 and confusion. Negative priming is generally a change of substrate by SOM consumers
442 who switch to LOM when enough nutrients are available without a necessary increase in
443 microbial activity. This mechanism is known as preferential substrate utilization
444 hypothesis (Sparling et al., 1982) and is often used to explain negative priming (Cheng,
445 1999; Guenet, et al., 2010b). Furthermore, positive priming is necessarily a consequence

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

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

460

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468

469 LFS and BG designed the study. LFS compiled and preprocessed the data. NACM wrote
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472

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751

752 **Figures legends**

753

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

759

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

764

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

769

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

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

782

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

797

798 **Figure 6** – Variation in the PRR according to (a) the duration of the experiment and (b)
799 the temperature at the time of the experiment. A positive PRR indicates that the addition
800 of labile organic matter accelerated the decomposition of the stable organic matter, while
801 negative values indicate the opposite. The solid line represents the predicted relationships
802 between PRR and each predictor variable according to a mixed-effects meta-analysis
803 model, and the dashed lines represent its 95% confidence intervals.
804

Figure 1.

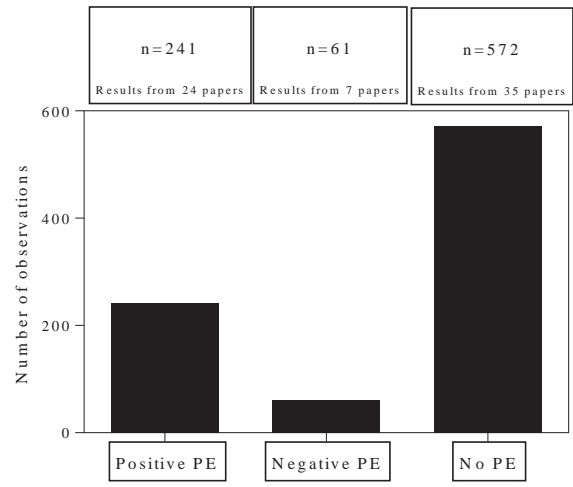


Figure 2.

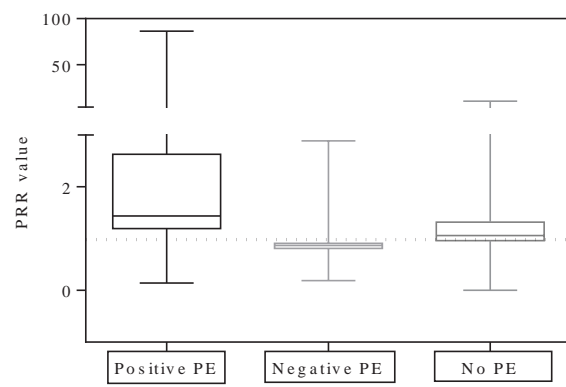


Figure 3.

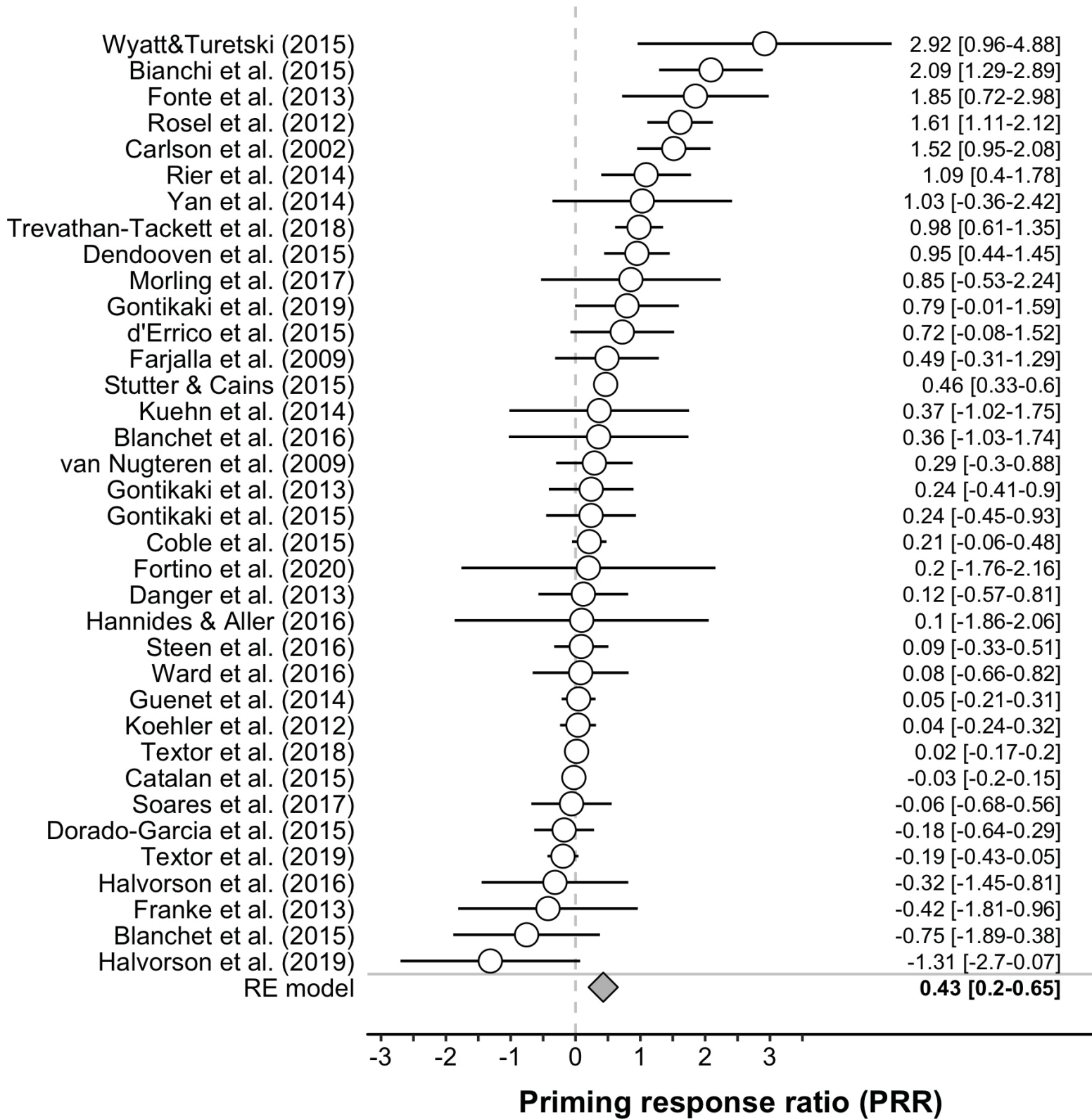


Figure 4.

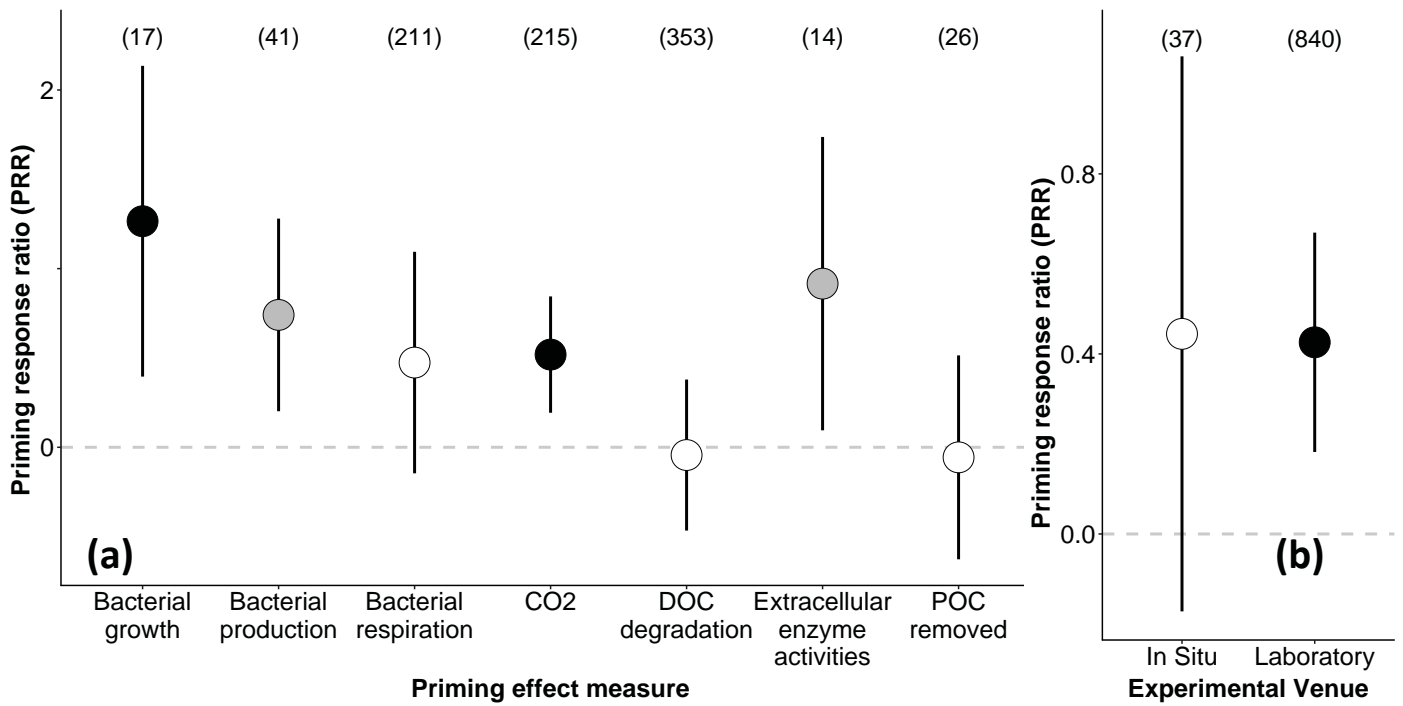


Figure 5.

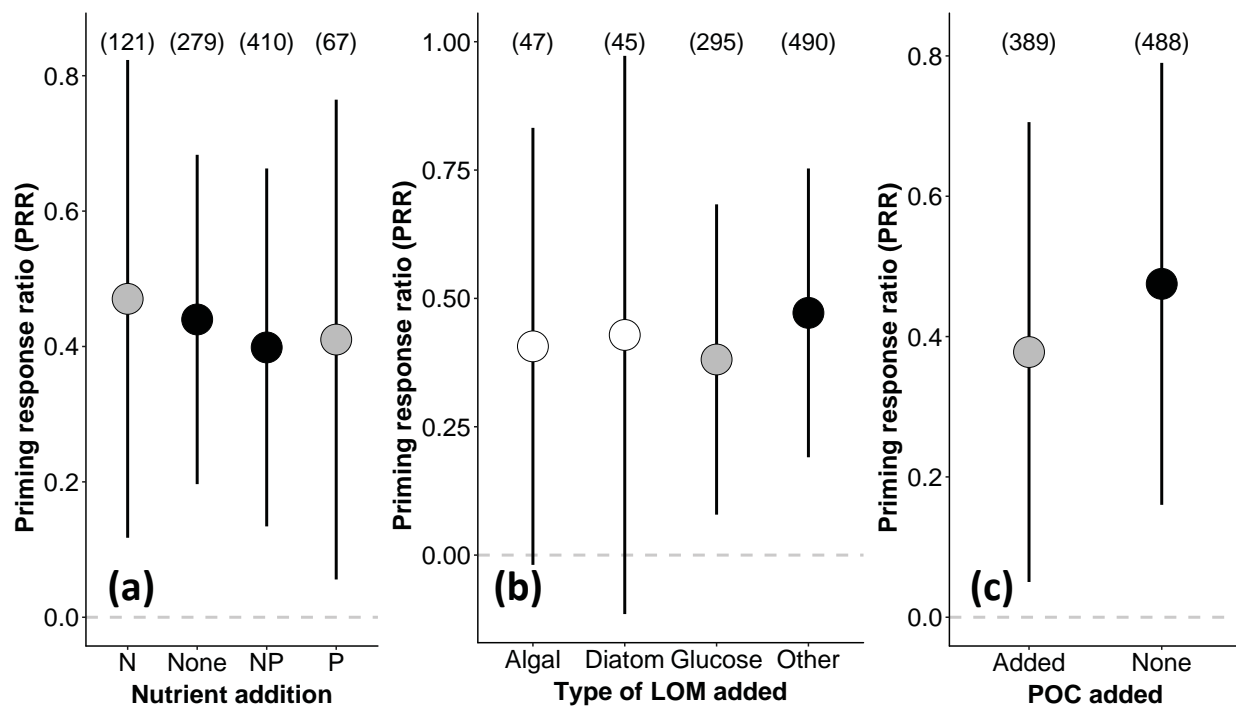
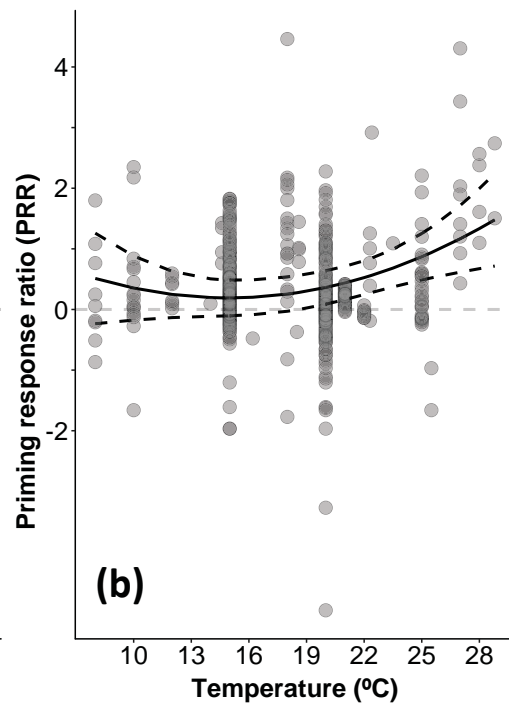
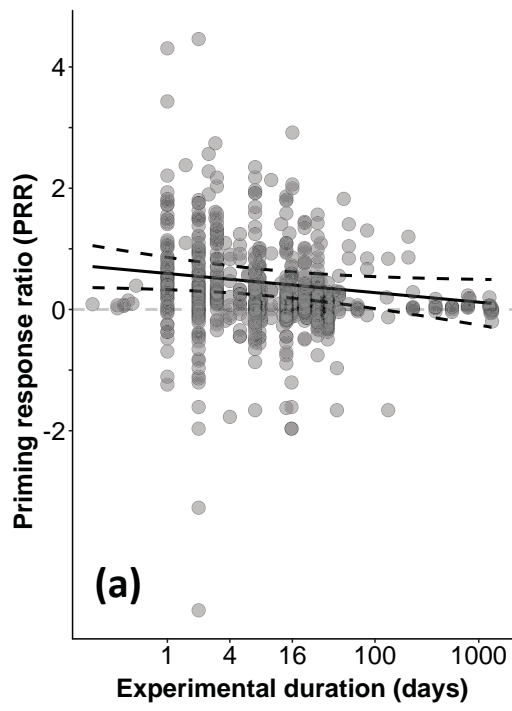


Figure 6.



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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