Bioturbation has a limited effect on phosphorus burial in salt marsh sediments

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Abstract. It has been hypothesised that the evolution of animals during the Ediacaran-Cambrian transition had a major impact on atmospheric O_2 and CO_2 concentrations. The models upon which this hypothesis rests, critically assume that bioturbation by the newly evolved fauna increased the burial of organic phosphorus (P_{org}) within the seafloor, relative to organic carbon (C_{org}) and that inorganic phosphorus (P_{inorg}) burial was not affected by bioturbationstimulated the burial of phosphorus

- 5 in marine sediments. This assumption is centrally based on data compilations from marine sediments deposited under oxic and anoxic bottom waters. Since anoxia excludes the presence of infauna and sediment reworking, the observed differences in P burial are assumed to be solely driven by the presence of bioturbators. This reasoning however ignores the potentially confounding impact of bottom water oxygenation on phosphorus burial. Here, our goal is to provide a field verification for test the idea that bioturbation increases the relative burial of organic phosphorus, and inorganic phosphorus (*P*_{org} and *P*_{inorg}).
- 10 respectively), while accounting for bottom water oxygenation. We present solid-phase phosphorus speciation data from salt marsh ponds with and without bioturbation (Blakeney salt marsh, Norfolk, UK). In both cases, the pond sediments are exposed to oxygenated bottom waters and so the only difference is the presence/absence of bioturbating macrofauna. Our data reveal that both the C_{org} : P_{org} ratio of buried organic matter and the rate of the rate of P_{org} and P_{inorg} burial are indistinguishable between bioturbated and non-bioturbated sediments. The A large terrestrial fraction of organic matter and higher sedimentation
- 15 velocity than generally found in marine sediments $(0.3 \pm 0.1 \text{ cm yr}^{-1})$ may partially impact these results. However, the absence of a clear effect of bioturbation on total P burial implies that previous studies may have overestimated the impact of the rise of bioturbation on atmospheric O_2 and CO_2 concentrations in the early Cambrian puts into question the presumed importance of bioturbation for phosphorus burial.

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1 Introduction

The evolution of animals near the Ediacaran-Cambrian transition (~542 million years ago - Ma) was a major evolutionary event in Earth's history (Mangano and Buatois, 2017; Meysman et al., 2006; Wood et al., 2019). Early benthic animals developed the ability to burrow (the so-called 'burrowing revolution'; Meysman et al., 2006), which profoundly changed the geochem-

5 ical cycling and burial of elements in the seafloor (Aller, 1977; McIlroy and Logan, 1999; Meysman et al., 2006). Benthic fauna affect the seafloor in two separate ways; by reworking of solid-phase particles (bio-mixing) and by flushing of burrows (bio-irrigation), lumped together under the term 'bioturbation' (Kristensen et al., 2012). Bio-mixing and bio-irrigation can have distinct effects on organic carbon mineralisation and early diagenesis (Kostka et al., 2002; van de Velde and Meysman, 2016) . For instance, bio-irrigation can promote aerobic respiration by flushing oxygenated bottom waters into deeper anoxic horizons

10 (Archer and Devol, 1992; van de Velde and Meysman, 2016), whereas bio-mixing transports fresh organic from the sediment-water interface into the anoxic zone, thus stimulating anaerobic mineralisation pathways (Berner and Westrich, 1985; van de Velde and Meysman

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Burial of carbon (C) and phosphorus (P)within marine sediments plays Bioturbation has been proposed to play a key role in the long-term functioning of the Earth system through regulation of atmospheric O_2 and CO_2 concentrations (Bergman et al., 2004; Berner,

- 15 . Therefore, an important open question is to what extent the burrowing revolution may have affected marine C and P burial sedimentary phosphorus (P) cycle. Via bio-mixing, bioturbating organisms transport P that is adsorbed on iron oxides from the oxic zone at the sediment surface into deeper sedimentary layers (Slomp et al., 1996). In the anoxic zone of the sediment, these iron oxides are reduced, and P is released further away from the sediment-water interface (SWI). Accordingly, P is retained longer in the sediment, which could stimulate the precipitation and eventual burial of inorganic P (Pinorg)
- 20 minerals, such as apatite (Slomp et al., 1996). Via bio-irrigation, benthic fauna can increase the availability of oxygen in the sediment (Volkenborn et al., 2019), which could stimulate the production of microbial polyphosphate compounds within the sediment column (Dale et al., 2016). Microbial polyphosphates are generated during the breakdown of organic matter under oxic conditions (Diaz et al., 2008), and can be converted into more refractory organic P (P_{org} ; as for example phosphate esters or phosphonates) or inorganic P minerals during diagenesis, which would then constitute a permanent P_{org} burial sink
- 25 (Berner et al., 1993; Van Cappellen and Ingall, 1994; Diaz et al., 2008; Goldhammer et al., 2010; Ingall and Jahnke, 1997). Overall, bioturbation could increase the burial of organic and inorganic P in the sediment. Accordingly, and whether this impact was substantial enough to influence the atmospheric composition and climate in the early Cambrian. In recent modelling studies, it has been hypothesised that the rise of bioturbation may have increased atmospheric CO₂ concentrations and decreased atmospheric O₂ concentrations, thus inducing warmer climatic conditions and more widespread ocean anoxia
- 30 (Boyle et al., 2014; van de Velde et al., 2018). These modelled effects are, however, critically dependent on the way that the effect of bioturbation on phosphorus burial in coastal and shelf sediments is described (Boyle et al., 2014; van de Velde et al., 2018)
 The key assumption is that bioturbation decreases the carbon-to-phosphorus ratio of the organic matter (C_{org} : P_{org}) that is buried in marine sediments. The additional removal of P then decreases productivity in the ocean (which is P-limited), at the Ediacaran-Cambrian boundary increased the burial of P in marine sediments (Boyle et al., 2014; Dale et al., 2016; van de Velde et al., 2018)

. Marine P burial plays a key role in the long-term functioning of the Earth system, because P is considered the long-term limiting nutrient for marine primary productivity (Van Cappellen and Ingall, 1996). If more P becomes buried, photosynthesis would decrease, thereby limiting the overall burial of organic carbon C_{org} in the seafloor, which subsequently increases subsequently increasing atmospheric CO_2 and lowers lowering atmospheric O_2 (Boyle et al., 2014; van de Velde et al., 2018)

5 . A second (and implicit) assumption is that bioturbation does not directly affect the burial of inorganic phosphorus (*P*_{inorg}). Instead, *P*_{inorg} burial is assumed to only depend on the amount of organic matter that rains down on the sediment (Boyle et al., 2014)

Neither of these assumptions have been extensively verified under field or laboratory conditions. The first assumption (bioturbation lowers the C_{org} : P_{org} of buried organic matter) is based on a data compilation from present-day sediments

- 10 deposited under oxic versus anoxic water columns. Sediments deposited under an oxygenated water column typically have a lower Corg : Porg (range: 30-250) than sediments deposited under an anoxic water column (range: 300-700) (Slomp and Van Cappellen, 200 . Within the present-day seafloor, sediments deposited under oxic conditions generally experience bioturbation (Levin et al., 1991) , and so it is argued that the observed differences in Corg : Porg are primarily the consequence of bioturbation, and less due to differences in the redox state (i.e. the oxygenation) of the overlying water (Boyle et al., 2014; Dale et al., 2016). The
- 15 second assumption (bioturbation does not affect the burial of inorganic phosphorus) is based on the argument that the burial of inorganic phosphorus in (Bergman et al., 2004; Berner, 1982). Hence, the form of minerals such as apatite $(Ca_5(PO_4)_3(F,Cl,OH))$ is predominantly controlled by the organic matter input into the sediment. A higher input rise of bioturbation may have increased atmospheric CO_2 concentrations and decreased atmospheric O_2 concentrations, thus inducing warmer climatic conditions and more widespread ocean anoxia (Boyle et al., 2014; van de Velde et al., 2018).
- 20 However, other factors play an important role for the burial of P in marine sediments. High sedimentation velocities stimulate the preservation of organic matter leads to higher mineralisation, thus inducing phosphate to be released in the pore water, which then leads to more precipitation and subsequent burial of phosphate as apatite (Ruttenberg and Berner, 1993). Nevertheless, other studies have argued that bioturbation increases the burial(Canfield, 1994), causing less mineralisation of authigenic apatite (Dale et al., 2016; Zhao et al., 2020) via the downward mixing of the iron oxides on which phosphate is adsorbed
- 25 (Slomp et al., 1996). Introducing iron oxides at depth releases phosphate further away from the sediment-water interface (SWI), organic matter, and provides additional adsorption sites for phosphate released from organic matter. Accordingly, phosphate is potentially retained longer in the sediment, which could stimulate the precipitation and eventual burial of inorganic phosphorus minerals (Slomp et al., 1996)consequently more burial of P_{org} associated with organic matter. Additionally, bottom water redox conditions are important for P burial; sediments underlying oxic bottom waters generally show higher burial rates of P_{org}
- 30 than sediments underlying anoxic bottom waters (Ingall and Jahnke, 1997; Ruttenberg, 2014; Slomp and Van Cappellen, 2007) , as sediments underlying oxic bottom waters likely receive an extra source of P_{org} in the form of microbial polyphosphates (Diaz et al., 2008). It is difficult to disentangle the confounding effect or sediment accumulation, redox conditions and bioturbation, because within the present-day seafloor, most sediments deposited under oxic conditions generally also experience bioturbation (Levin et al., 1991). As a result, the proposed effect of bioturbation on P burial has not been extensively verified under field or
- 35 laboratory conditions.

To be able to adequately tease apart the impact of bioturbation from other confounding factors(such as the redox conditions at the SWI or organic matter input), one requires sites that have oxygenated waters and a similar input of organic matter, but no bioturbation. While these conditions are extremely rare in the modern seafloor, they are found in salt marsh ponds along the North Sea coast of Norfolk (UK), which contain sediments with overlying oxygenated water that are either bioturbated or

- 5 non-bioturbated (Antler et al., 2019; Hutchings et al., 2019). These two different sediment types can be found in neighbouring ponds, less than five meters apart, and no systematic difference in local sediment input, organic matter supply or other boundary conditions has been found between the two pond types (Antler et al., 2019; Hutchings et al., 2019; van de Velde et al., 2020). This remarkable biogeochemical dichotomy between the pond sediments has recently been attributed to alternative stable states, in which small initial differences between ponds are amplified through non-linear positive feedbacks in the sedimentary
- 10 iron-sulphur cycle (van de Velde et al., 2020).

Whatever the cause of the biogeochemical dichotomy, the important aspect here is that by comparing the geochemistry of the two oxygenated pond types, we can single out the effect of burrowing fauna on sediment biogeochemistry. These ponds within the Norfolk salt marsh complex, hence, provide a unique environment to study the impact of bioturbation on the burial of organic and inorganic phosphorus, without the confounding effect of bottom water oxygenation. To this end, we collected solid-

15 phase phosphorus data during three separate visits and quantified the burial rates of P in the bioturbated and non-bioturbated ponds.

2 Materials and Methods

2.1 Field site

- Blakeney salt marsh (Fig. 1) is part of a larger salt marsh complex along the North Sea coast of East Anglia (UK). The higher, vegetated, marsh hosts several shallow, water-filled ponds with a surface area of $\sim 50 - 500 m^2$ and a water depth of 10 - 20 cm (Fig. 1; van de Velde et al., 2020). These ponds show a conspicuous dichotomy in terms of their sediment geochemistry, and belong to either one of two end-member types. Pond sediments are either heavily bioturbated and the solid phase is rich in iron oxides, or sediments are non-bioturbated and the pore water is rich in hydrogen sulphide (Antler et al., 2019; Hutchings et al., 2019; van de Velde et al., 2020). The bioturbated ponds are colonised by large macrofauna, mostly Nereis and Arenicola,
- at high densities (~1000 organisms m^{-2} ; Antler et al., 2019), while the non-bioturbated sediments do not show signs of macrofauna or burrows. Water column concentrations of oxygen, DIC and nutrients are not statistically different between pond types, and both types of ponds have the same sedimentation flux $(0.9 \pm 0.1 kgm^{-2}yr^{-1})$, indicating they receive a similar input of detrital minerals. Furthermore, all ponds display similar inputs of organic matter, thus suggesting that the only important difference between the ponds is the presence of burrowing fauna (van de Velde et al., 2020). Depth profiles of ¹³⁷Cs show a
- 30 well-defined peak in the non-bioturbated ponds, suggesting they have been undisturbed by fauna for at least 60 years (van de Velde et al., 2020).



Figure 1. Overview of the field site in the Blakeney saltmarsh system, UK. Sampled ponds are outlined in white (non-bioturbated) and blue (bioturbated), with ponds where sediment cores taken denoted with the sampling year. Coordinates of the sampled ponds are given in Table A1. (b,c) Map data ©2020 Google.

2.2 Sediment sampling and analysis

Sediment cores were collected on three separate visits (October 2015, August 2016 and August 2018). Twelve ponds were examined in total (sampling sites are indicated in Fig. 1). During each sampling campaign, two replicate sediment cores were collected from each sampled pond. Core sectioning was done at 0.5 cm resolution from 0 to 3 cm depth, at 1 cm resolution
between 3 and 8 cm depth, and in 2 cm slices from 8 to 22 cm depth. Sediment sections were collected in 50 mL centrifuge tubes (polypropylene; TPP, Switzerland). In 2015 and 2016, sediment cores were processed under anaerobic conditions in a glove bag with N₂, freeze-dried and stored in a sealed aluminium bag under N₂ atmosphere for later solid-phase analysis. In 2018, cores were immediately sliced in open air in the field, and subsequently freeze-dried and stored under room conditions in 50 mL centrifuge tubes. This difference in sampling procedure reflects the subsequent analyses. In 2015 and 2016, solid

10 phase was analysed for different phosphorus fractions following the SEDEX phosphorus extraction (Ruttenberg, 1992; Slomp et al., 1996). In 2018, due to the higher amount of samples, we decided to use a simpler and faster extraction method that only differentiates between inorganic and organic phosphorus fractions (Bowman, 1989; Olsen and Sommers, 1982).

Sediment samples from all three campaigns were analysed for carbon and nitrogen content. To this end, freeze-dried solid phase samples were ground to a fine powder and analysed by an Interscience Flash 2000 organic element analyser (precision <5%) for determination of particulate organic carbon (POC) and total nitrogen (TN). Before analysis, samples for POC were first acidified with 0.1M HCl to remove the inorganic carbon (Nieuwenhuize et al., 1994). Concentrations of POC and TN are

5 expressed as mass % of dry sediment. Organic matter C_{org} : N_{tot} was calculated as the molar ratio of POC over TN. The POC and TN results have been presented previously in van de Velde et al. (2020).

The SEDEX procedure used in 2015 and 2016 separates total sedimentary P in 5 fractions; exchangeable P (P_{exch}), P associated with iron (P_{Fe}), authigenic P (P_{auth}), detrital P (P_{det}) and P associated with organic matter (P_{org}). All extractions were performed on a subsample of 300 mg, under room temperature and under constantly agitated conditions (the extraction procedure is detailed in Table A2). Inorganic phosphorus (P_{inorg}) is calculated as

$$P_{inorg} = P_{exch} + P_{Fe} + P_{auth} + P_{det} \tag{1}$$

and expressed as μ mol g⁻¹ dry sediment. The extraction procedure used in 2018 separates the sediment phosphorus content in 2 fractions; total phosphorus (P_{tot}) and inorganic phosphorus (P_{inorg}), organic phosphorus is then calculated as the difference between P_{tot} and P_{inorg} (Bowman, 1989; Olsen and Sommers, 1982). Extractions were performed on a subsample of 1 g, under room temperature and under constantly agitated conditions (extraction procedure detailed in Table A2).

2.3 Burial fluxes and solid phase inventories

Burial fluxes of solid phase species were calculated based on the sedimentation flux (J_{sed}) and the concentration of the solid component at the bottom of the sediment column (C_{solid}) :

$$J_{burial} = J_{sed}C_{solid} \tag{2}$$

20 The sedimentation flux was previously determined based on ${}^{210}Pb$ and ${}^{137}Cs$ dating, and was statistically indistinguishable between pond types (0.9 \pm 0.1 kg m⁻² yr⁻¹; van de Velde et al., 2020).

Solid phase inventories were calculated by integrating measured concentrations over the first 20 cm of the sediment cores:

$$INV = \rho_{solidphase} \int_{x_{down}}^{x_{up}} (1 - \phi_x) C_{solid} dx$$
(3)

Where ϕ_x is the porosity at depth x and $\rho_{solidphase}$ the solid phase density (previously determined to be 2.2 g cm⁻³; van de Velde et al., 2020). The porosity depth profile was determined from the water content and solid-phase density, considering the salt content of the pore water. The water content of the sediment was determined as the difference in sediment weight before and after freeze-drying. Porosity profiles have been presented previously in van de Velde et al. (2020).

2.4 Statistics

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The measured values of C_{org} : N_{tot} and C_{org} : P_{org} , calculated burial fluxes of P_{org} and P_{inorg} and solid-phase inventories 30 were averaged over the duplicate cores from each pond and one-way ANOVA's were used to test for significant differences between bioturbated and non-bioturbated ponds. Due to the different methods used for P extraction in 2015 and 2016 relative to 2018, the inclusion of the sampling year as a random effect was tested through model evaluation using AIC (Akaike information criterion). Sampling year was not significant for all dependent factors, and so it was excluded from subsequent analyses. Residuals were tested for normality and homoscedasticity, and all but $C_{org} : P_{org}$ fulfilled these assumptions. The values of $C_{org} : P_{org}$ were log transformed before analysis.

3 Results

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3.1 Bioturbation $\frac{1}{C_{org}}$: P_{org} values and organic phosphorus burial

Individual depth profiles of solid-phase variables (POC, TN, POPTP, POP, PIP) show variation within the sediments of a given pond type, indicating spatial heterogeneity (Fig. 2). Still, averaged depth profiles of the six non-bioturbated and the six bio-

- 10 turbated ponds reveal that bioturbated non-bioturbated sediments have generally a stronger down-core gradient in POC, TN and POP (Fig. 2A-FA-J), which is expected as sediment bio-mixing by bioturbating fauna acts to erase solid phase gradients (van de Velde and Meysman, 2016). Differences in POC, TN and POP inventories in the top 20 cm between bioturbated and non-bioturbated cores are insignificant (Fig. 2A-FA,D,G,H; Table A4). Consistently, $C_{org} : N_{tot}$ and $C_{org} : P_{org}$ values are not significantly different between bioturbated and non-bioturbated pond types (p > 0.1; Table A4). Values of $C_{org} : N_{tot}$ range
- 15 from 9 to 15, with an average value of 12 (2GFig. 2K). These values are slightly higher than expected for sediments from fully marine settings ($C_{org} : N_{tot} < 10$; Burdige, 2006), but are consistent with sediments from temperate salt marshes, which generally have $C_{org} : N_{tot}$ values of 10 or higher (2Spivak et al., 2018)(Spivak et al., 2018). Similarly, $C_{org} : P_{org}$ values averaged around 500 in both the non-bioturbated and bioturbated sediment cores (2G). These $C_{org} : P_{org}$ values are higher than expected for marine sediments with similar sedimentation rates underlying oxygenated waters ($C_{org} : P_{org} \sim 200$; Slomp and
- Van Cappellen, 2007), and are more representative of low-oxygen and anoxic marine environments ($C_{org}: P_{org} = 300-700$; Slomp and Van Cappellen, 2007). However, since the pond waters were oxygenated at the time of sampling (van de Velde et al., 2020), the elevated $C_{org}: P_{org}$ values most likely reflect the contribution of plant material from the surrounding marsh ($C_{org}: P_{org} > 500$; Table A3), which is substantially elevated above the $C_{org}: P_{org}$ of marine plankton (~106; Redfield, 1934).
- Overall, our organic P data show two main findings: (i) bioturbated sediments have similar amounts of P_{org} ($P_{inv} = 0.067 \pm 0.005 \text{ mmol cm}^{-2}$; Fig. 3A) compared with non-bioturbated sediments ($P_{inv} = 0.072 \pm 0.004 \text{ mmol cm}^{-2}$; Fig. 2,3a), and (ii) $C_{org} : P_{org}$ values are not significantly lower in bioturbated sediments (relative to non-bioturbated sediments) (Fig. 2). This implies that the burial of differences in P_{org} burial in bioturbated sediments is comparable in bioturbated sediments, relative to non-bioturbated sediments (Fig. 3B). Indeed, the difference in P_{org} burial between bioturbated ($(17 \pm 4 \mu \text{mol m}^{-2} \text{ d}^{-1})$) and
- 30 are not statistically significant from non-bioturbated sediments (19 ± 2 μ mol m⁻² d⁻¹) ponds is not statistically significant ((Fig. 3B; p > 0.1; Suppl. Table A4).



Figure 2. Vertical solid phase profiles of (A,B) particulate organic carbon (POC), (C,D) total nitrogen (TN)and, (E,F) total phosphorus (TP), (G,H) particulate organic phosphorus (POP) and (LJ) particulate inorganic phosphorus (PIP). Individual cores are plotted as a light gray lines, and the average vertical profile over all cores is plotted as black dots. Values are averaged inventories and errors are 1 standard deviation. (GK) Boxplots of the $C_{org} : N_{tot}$ and $C_{org} : P_{org}$ of the particulate organic matter fraction.

3.2 Bioturbation and inorganic phosphorus burial

Our solid phase analyses show that bioturbated sediments $(30.203 \pm 10.70 \,\mu\text{mol g}^{-1}\text{cm}^{-2})$ contain significantly more particulate inorganic phosphorus than non-bioturbated sediments $(16-113 \pm 3.17 \,\mu\text{mol g}^{-1}\text{cm}^{-2})$ (p < 0.1; Fig. 3A21.3; Fig. 4A, F3A; Table A4).

- SEDEX extractions, performed on sediment cores collected in 2015 and 2016, show that the large difference in P_{inorg} is caused by the much higher P_{exch} and P_{Fe} contents in the bioturbated sediments (Fig. 4: $P_{exch} + P_{Fe}$ is up to 90 mmol P cm⁻² higher in the bioturbated sediments; Table A5). Phosphorus adsorbs adsorbed onto iron oxide minerals, which are introduced at depth is transported from the sediment-water interface to the deeper sedimentary layers by the downward mixing of benthic fauna (Slomp et al., 1996). Indeed, ~ 50% of the Fe minerals in the bioturbated sediments at Blakeney salt marsh are in
- 10 oxidised form, whereas < 10% are in the non-bioturbated sediments (see van de Velde et al. (2020) for an extended discussion of the Fe-S cycle at the field site).</p>

The increased inventory of P_{exch} and P_{Fe} at depth seemingly does not lead to more precipitation of P_{auth} (Table A5), since we do not find detectable formation of authigenic apatite, the concentrations of which are negligible throughout all sediment cores in both ponds (< 1 µmol g⁻¹). The lack of measurable authigenic P formations is at odds with previous hypotheses

15 (Dale et al., 2016; Slomp et al., 1996). Potentially, the high concentrations of Fe^{2+} in the pore water of the bioturbated sediments (up to 300 μ M; van de Velde et al., 2020) promoted the formation of vivianite over apatite (Ruttenberg, 2014). Because vivianite



□ Non-bioturbated ■ Bioturbated

Figure 3. Boxplots of (A) inventories and (B) burial rates of inorganic and organic P fractions. The data of 2015 are not included in panel A, since some depth samples were not analysed for P fractionation.

is extracted in the P_{Fe} fraction (Nembrini et al., 1983), we cannot separate between P associated with iron oxides, and P in the form of vivianite. The precipitation of vivianite in the bioturbated sediments could potentially stimulate the burial of P_{inorg} , but this effect is not readily seen in our data. While P_{inorg} concentrations are high in the top layers, they strongly decrease with depth, thus P_{inorg} is not efficiently buried. Overall, we find that the burial rate of P_{inorg} is $38 \pm 3 \ \mu \text{mol m}^{-2} \ d^{-1}$ in bioturbated sediments, and $36 \pm 3 \ \mu \text{mol m}^{-2} \ d^{-1}$ in the non-bioturbated sediment, and this difference is not significant (p > 0.1; Table A4).

4 Discussion

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By comparing non-bioturbated and bioturbated sediment cores collected from an East Anglian salt marsh, this study provides a field verification for two existing hypotheses: (1) bioturbation does not significantly affect the hypothesis that bioturbation

10 stimulates the burial of inorganic P minerals and (2) bioturbation increases the burial of organic phosphorus relative to organic earbon. Related to the first hypothesis, our and organic P minerals. Our field data show that a bioturbated sediment contains more inorganic P, which exists mainly in the form of iron-associated P. Nevertheless, the accumulation of inorganic P occurs principally in the top layers of the sediment. At 20 cm, the P_{inorg} levels in bioturbated sediments decrease to similar



Figure 4. Vertical solid phase profiles of (A,F) particulate inorganic phosphorus (PIP). Values are depth-averaged concentrations. (B)-(E), (G)-(J) Solid phase phosphorus speciation (SEDEX) of cores collected in 2015 and 2016. P_{exch} =exchangeable phosphorus, P_{Fe} =iron-bound phosphorus, P_{auth} =authigenic phosphorus, P_{det} =detrital phosphorus, P_{org} = organic phosphorus. Note that the P_{auth} fraction is too small to be visible on the figure.

levels as in non-bioturbated sediments (Fig. 4). We find no evidence for the formation of authigenic P (Fig. 4), which is at odds with previous hypotheses (Slomp et al., 1996; Zhao et al., 2020). Potentially, the high concentrations of Fe²⁺ in the pore water of the bioturbated sediments (up to 300 μ M; van de Velde et al., 2020) promoted the formation of vivianite over apatite (Ruttenberg, 2014). Because vivianite is extracted in the P_{Fe} fraction (Nembrini et al., 1983), we cannot separate between P

- 5 associated with iron oxides, and P in the form of vivianite. The precipitation of vivianite in the bioturbated sediments could potentially stimulate the burial of P_{inorg} , but this effect is not readily seen in our data. As a consequence, we find that the burial of P_{inorg} was not significantly different between bioturbated and unbioturbated ponds, which does not support the idea that bioturbation stimulates the burial of inorganic P minerals. Our data are hence not congruent with previous modelling and field studies that have suggested that bioturbating fauna stimulates the burial of authigenic apatite (Slomp et al., 1996; Zhao
- 10 et al., 2020). These studies argued that bioturbators mix iron oxides, on which phosphate is adsorbed, further away from the sediment-water interface (SWI), increasing the retention time of phosphate in the sediment, and subsequently stimulating the precipitation and eventual burial of inorganic phosphorus minerals (Slomp et al., 1996; Dale et al., 2016). Bioturbators also flush their burrows however, which removes phosphate from the pore water (Dale et al., 2016). Consequently, depending on the animals animal community (irrigation versus mixing), the pore water can become undersaturated with respect to apatite,
- 15 leading to lower precipitation rates and burial of apatite. The difference between oxic, bioturbated and oxic, non-bioturbated sediments inferred from the model study of Dale et al. (2016) is only a few μ mol m⁻² d⁻¹, which is likely undetectable in a field study like ours (Fig. 3). Consequently, our results suggest that the effect of bioturbation on P_{inorg} minerals is small, consistent with diagenetic modelling results (Dale et al., 2016).

Related to the second hypothesis, we We find that the C_{org} : P_{org} of buried organic matter burial of P_{org} is indistinguishable 20 between bioturbated and non-bioturbated sediments (Fig. 2G). Accordingly, our field data do not support the idea that bioturbation increases the relative burial of organic phosphorus. It should be noted however that the C_{org} : P_{org} values recorded here are relatively high, and amount to ~ 500 in both the non-bioturbated and bioturbated sediment cores (Fig. 2G). These C_{org} : P_{org} values are higher than expected for marine sediments underlying oxygenated waters, and deviate considerably from the C_{org} : P_{org} values 70-100 in oxic sediments obtained in the model study of Dale et al. (2016). One reason for this is that the sedimentation velocity in Norfolk salt marsh ponds is relatively high (0.3 cm yr⁻¹, compared to a mean value of 0.1 cm yr⁻¹ for shelf sedi . High sedimentation velocities stimulate the preservation of organic matter (Canfield, 1994), and hence cause less mineralisation

- 5 of C_{org} , thus leading to higher C_{org} : P_{org} values. But even when compared to sediments with similar sedimentation rates underlying oxygenated waters (C_{org} : $P_{org} \sim 200$; Slomp and Van Cappellen, 2007), the values remain high. The C:N:P ratios of the organic matter in the ponds-salt marsh pond sediments suggests a large contribution of plant material from the surrounding marsh (Fig. 2), which has elevated C:N:P ratios compared to marine organic matter (Suppl., Table A3). Because terrestrial material is less easily degraded than marine organic matter, the addition of plant material to the sediment organic matter pool
- 10 dilutes the signal of the marine organic matter (Ruttenberg, 2014). This presence of terrestrial vegetation explains the high C_{org} : P_{org} values recorded here. But still, the observation remains: even in these sediments with high C_{org} : P_{org} values, there is no difference in C_{org} : P_{org} values between bioturbated and non-bioturbated sediments., which could explain why we see no effect of bioturbation. Another possible reason is that the sedimentation velocity in Norfolk salt marsh ponds is relatively high (0.3 cm yr⁻¹, compared to a mean value of 0.1 cm yr⁻¹ for shelf sediments; Burwicz et al., 2011). High sedimentation velocities
- 15 stimulate the preservation of organic matter (Canfield, 1994), and would potentially further dilute the effect of bioturbation on *Porg* burial. Nevertheless, the POC profiles suggest an appreciable amount of organic matter is being degraded in the salt marsh pond sediments (Fig. 2). Indeed, organic matter mineralisation rates based on POC and nutrient profiles range from 6-38 mmol C m⁻² d⁻¹, which is comparable to rates observed in shallow marine sediments (Burdige, 2007) and thus indicates that the Blakeney salt marsh site shows a comparable metabolic activity to marine sediments. The observation then still remains;
 22 bit to be the summariant for the summariant profiles and the summariant profiles.
- 20 <u>bioturbation seems to have no significant impact on *P*org burial.</u>

Low C_{org} : P_{org} values observed in Phanerozoic sediments deposited under oxygenated conditions have initially been attributed to different water column redox conditions (Ingall and Jahnke, 1997; Slomp and Van Cappellen, 2007; Ruttenberg, 2014) . The mechanism behind this remains still somewhat elusive, but could be related to Bioturbation is believed to impact P_{org} . burial by stimulating the formation of microbial polyphosphates, which are generated during the breakdown of the settling

- 25 organic matter under oxic conditions (Diaz et al., 2008). During diagenesis, these polyphosphate molecules would then be converted into can act as an intermediate for the formation of apatite or more refractory organic P (as for example phosphate esters or phosphonates), which then constitutes a permanent P_{org} sink (Berner et al., 1993; Van Cappellen and Ingall, 1994; Ingall and Jahr . Because Phanerozoic sediments that are deposited under oxygenated conditions are virtually always bioturbated, more recent studies have argued that the decreased C_{org} : P_{org} values in Phanerozoic sediments are related to bioturbation, rather than water
- 30 column redox conditions (Boyle et al., 2014). However, the diagenetic model results of Dale et al. (2016) show that , while Corg : Porg values in oxic, bioturbated sediments are indeed much lower than in anoxic sediments (~ 70 compared to ~ 500), the difference between oxic, bioturbated and oxic, compounds (Berner et al., 1993; Goldhammer et al., 2010). Polyphosphates are formed during aerobic respiration of organic matter (Diaz et al., 2008), and because bio-irrigation stimulates aerobic respiration in the sediments (Archer and Devol, 1992; van de Velde and Meysman, 2016), it has been hypothesised that more
- 35 polyphosphates could be formed in bioturbated sediments (Dale et al., 2016). However, other studies have shown that polyphosphates

and the subsequent conversion to apatite also occurs under anoxic conditions (Goldhammer et al., 2010), so it is questionable whether periodic influshing of oxygenated water would have a large impact on polyphosphate formation. Unfortunately, our analysis method does not allow us to differentiate between bulk organic P and microbial polyphosphates to investigate whether polyphosphate formation plays a role in both bioturbated and non-bioturbated sediments is much smaller (\sim 70 compared to \sim

- 5 100). These modelled C_{org} : P_{org} values suggest that the effect of bioturbation is much smaller than the effect of water column redox, and agrees with the observations made here. The high C_{org} : P_{org} values reported from anoxic sediment are hence not due a lack of bioturbation, but rather due to a redox effect, where the absence of oxygen stimulates the preservation of organic matter (increasing C_{org}), and reduces the formation of polyphosphates by micro-organisms (decreasing P_{org}). sediments. This would be an interesting avenue for future research.
- Still, a A number of caveats need to be taken into account when interpreting our results, as observations made in the surface sediments of the Norfolk salt marsh ponds are not necessarily representative of burial signals made at several metres deep in coastal and shelf sediments. As noted above, the $C_{org} : P_{org}$ ratio of buried organic matter is high, as it is influenced by the deposition of the salt marsh vegetation with high C:P ratios, and therefore, caution is required when extrapolating our results to other coastal and shelf sediments. A difference in time scale could be another reason for the discrepancy between
- 15 our field observations and the lower C_{org} : P_{org} values reported elsewhere in the literature. The data reported in the literature are collected from geological formations (see, e.g., Ingall et al., 1993) or deep drill cores (see, e.g., Slomp et al., 2004). These samples have undergone several hundreds to thousands years of diagenesis before being sampled and analysed. In contrast, based is another caveat to take into account. Based on an average sedimentation velocity of 0.3 cm yr⁻¹ measured via radionuclide dating (van de Velde et al., 2020), our samples represent only 60 years of sediment accumulation and they hence
- 20 indicate that, after ~ 60 years of early diagenesis, there is no discernible difference in burial of P minerals. Diagenesis later in the burial history could still affect long-term P burial. Data reported in the literature are collected from geological formations (see, e.g., Ingall et al., 1993) or deep drill cores (see, e.g., Slomp et al., 2004). These samples have undergone several hundreds to thousands years of diagenesis before being sampled and analysed. However, we cannot see a mechanism via which bioturbation could have an imprint on the sediment that eventually leads to differential diagenesis of P minerals.
- 25 later in their burial history. If bioturbation does not already create a difference within C_{org} : P_{org} values in in P burial in the early phase of diagenesis, it is highly unlikely that will happen afterwards. So the difference in time scale cannot explain why C_{org} : P_{org} values easily explain why P burial rates are similar in bioturbated and non-bioturbated sediments.

Overall, more field studies and laboratory experiments are required to verify our results. Nevertheless, the absence of a clear impact of bioturbation on P burial questions whether the modelled effects of the evolution of bioturbation in the early

30 Cambrian, if they are <u>solely</u> based on inferred effects on C:P values of buried organic matter<u>of</u> bioturbation on P burial, do not overestimate the true impact of the 'burrowing revolution'. Our study highlights that assumptions made in Earth System models should be firmly grounded in field observations, before accurate inferences about large-scale questions can be made, such as the impact of the burrowing revolution on the composition of the atmosphere and climate.

Table A1. Coordinates and type of the ponds sampled in the 2015, 2016 and 2018 field campaigns in the Blakeney salt marsh. See Fig. 1c	in
the main text for relative geographical location of the ponds.	

	Coordinates	Туре	Year sampled
1	52° 57' 22.7"N 01° 00' 14.0"E	Bioturbated	2015
2	$52^{\circ} 57' 23.0"N 01^{\circ} 00' 14.0"E$	Unbioturbated	2015
3	52° 57' 22.2"N 01° 00' 16.6"E	Bioturbated	2016
4	$52^{\circ} 57' 24.0"N 01^{\circ} 00' 16.0"E$	Unbioturbated	2016
5	52° 57' 25.2"N 01° 00' 13.2"E	Bioturbated	2018
6	52° 57' 25.3"N 01° 00' 12.5"E	Bioturbated	2018
7	52° 57' 24.6"N 01° 00' 10.6"E	Bioturbated	2018
8	52° 57' 24.3"N 01° 00' 10.9"E	Bioturbated	2018
9	52° 57' 24.7"N 01° 00' 13.4"E	Unbioturbated	2018
10	52° 57' 24.4"N 01° 00' 14.1"E	Unbioturbated	2018
11	52° 57' 24.3"N 01° 00' 9.9"E	Unbioturbated	2018
12	52° 57' 24.1"N 01° 00' 10.1"E	Unbioturbated	2018

Table A2. Specifics for the sequential extractions of phosphorus. After the extraction, the sample was centrifuged (2500g for 10 min) and the supernatant was filtered (0.45 μ m cellulose acetate).

Fraction	Extraction solution	Atmosphere	Time	Analysis			
SEDEX Phosphorus extraction (Ruttenberg, 1992; Slomp et al., 1996)							
P_{exch}	$1 \text{ M} MgCl_2$	N_2	30 min.	spectrophotometer			
P_{Fe}	12 g sodium dithionite in 480 mL sodium acetate (1M)	N_2	8 h	ICP-OES			
	+ 60 mL sodium bicarbonate (1 M)						
	+ wash: 1 M $MgCl_2$	N_2	30 min.	spectrophotometer			
P_{auth}	300 mL sodium acetate (1M) + 1700 mL acetic acid (1	open air	6h	spectrophotometer			
	M)						
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer			
P_{det}	1 m HCl	open air	24 h	spectrophotometer			
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer			
P_{org}	Combustion at 550°C	open air	2h				
	1 M HCl	open air	24 h	spectrophotometer			
	+ wash: 1 M $MgCl_2$	open air	30 min.	spectrophotometer			
One-step Phosphorus extraction (Bowman, 1989; Olsen and Sommers, 1982)							
Pinorg	1 M H ₂ SO ₄	open air	overnight	spectrophotometer			
P_{tot}	Combustion at 550°C	open air	1h				
	$1 \text{ M} H_2 SO_4$	open air	overnight	spectrophotometer			

Table A3. Summary of salt marsh plant properties. Data was first published in van de Velde et al. (2020)

Salt marsh properties								
	Suaeda mar- itima	Salicornia radicans	Spartina an- glica	Ameria mar- itima	Elytrigia atherica	Halimione portulacoides	Limonium vulgare	
$C_{org}: N_{tot}$	18	20	27	20	74	26	25	
$C_{org}: P_{org}$	682	492	669	554	1289	802	692	

One-way ANOVA							
	P_{inorg} burial rate	P_{org} burial rate	$C_{org}: N_{tot}$	$C_{org}: P_{org}$			
Pond type Mean square (df)	13.69 (1)	11.826 (1)	0.04417 (1)	0.0001 (1)			
Residuals Mean square (df)	6.59 (10)	9.768 (10)	0.22665 (10)	0.07641 (10)			
F-value	2.077	1.211	0.195	0.0			
р	0.18 0.297		0.668				
Pond type	95% Confidence Intervals						
Non-bioturbated	33.65, 38.32	16.38, 22.07	11.52, 12.39	6.04,6.54			
Bioturbated	35.79, 40.46	14.40, 20.08	11.40, 12.27	6.04,6.54			
	P _{inorg} inventory	P_{org} inventory	POC inventory	TN inventory			
Pond type Mean square (df)	20006 (1)	1.05 (1)	28.61 (1)	0.0033 (1)			
Residuals Mean square (df)	2847 (10)	75.8 (8)	132.14 (10)	0.6345 (10)			
F-value	7.026	0.014	0.217	0.005			
р	0.029	0.91	0.652	0.944			
Pond type 95% Confidence Intervals							
Non-bioturbated	58.26, 168.31	61.85, 79.81	72.40, 93.31	5.86,7.31			
Bioturbated	147.71, 257.77	61.20, 79.16	69.31, 90.22	5.82,7.27			

Table A4. Results from One-way ANOVA analysis and calculated 95% confidence intervals. Residuals were tested for normality and heterogeneity, all passed these assumptions except C:P, which was log-transformed.

Table A5. Inventories of the individual phosphorus fractions. P_{org} and P_{inorg} are reported as mean ± 1 s.d., SEDEX fractions are given as a range (due to the low number of replicates) from the 2016 cores (2015 was omitted because some depth samples were not analysed for P fractionation).

	P_{org}	P_{inorg}	Individual P _{inorg} fractions (only 2016)			
			P_{exch}	P_{Fe}	P_{auth}	P_{det}
	$mmol \ cm^{-2}$	$mmolcm^{-2}$	$\mu molcm^{-2}$	$\mu mol cm^{-2}$	$\mu molcm^{-2}$	$\mu mol cm^{-2}$
Non-bioturbated	0.071 ± 0.004	0.11 ± 0.02	0.13-0.19	30.1-32.2	2.4-3.8	100-103
Bioturbated	0.067 ± 0.009	0.20 ± 0.07	10.1-17.3	86.5-108	2.2-2.8	111-114

Author contributions. SJV conceived the hypothesis. SJV and FJRM organised the field sampling. All authors contributed to the field sampling. SJV and IC performed the SEDEX extractions. SJV analysed the data. RKJ did the statistical analyses. SJV and FJRM wrote the manuscript with input from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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