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Enhanced carbon burial in seagrass meadows under ocean acidification revealed by carbon dioxide vents

Theodor Kindeberg^{1*}, Núria Teixidó^{1,2}, Steeve Comeau¹, Jean-Pierre Gattuso^{1,3}, Beat Gasser⁴, Alice Mirasole², Samir Alliouane¹, Ioannis Kalaitzakis¹, Denisa Berbece⁵, Christopher Cornwall⁵, Pere Masque^{4,6}

¹ Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, 181 chemin du Lazaret, 06230 Villefranche-sur-Mer, France

² Stazione Zoologica Anton Dohrn, Ischia Marine Centre, Department of Integrated Marine Ecology, 80077 Ischia (Naples), Italy

³ Institute for Sustainable Development and International Relations, Sciences Po, 27 Rue Saint-Guillaume, 75007 Paris, France

⁴ International Atomic Energy Agency (IAEA), Marine Environmental Laboratories, Quai Antoine 1er, Monaco, Monaco

⁵ School of Biological Sciences and Coastal People Southern Skies Centre of Research Excellence, Victoria, University of Wellington, Wellington, New Zealand

⁶ Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Joondalup, WA, Australia

* Corresponding author: theodor.kindeberg@imev-mer.fr

Abstract

Seagrass meadows are natural carbon sinks, yet the effect of ocean acidification on their carbon burial capacity remains poorly understood.

Here we investigated natural carbon dioxide vents in Ischia, Italy to assess how seawater pH influences carbon burial in an area dominated by the seagrass *Posidonia oceanica*. Organic carbon burial rates (mean $\pm$ standard error) between 1954 – 2021 were low under ambient conditions ($1.5 \pm 0.5 \text{ g m}^{-2} \text{ yr}^{-1}$) but increased sharply under acidified conditions ($7 \pm 1 \text{ g m}^{-2} \text{ yr}^{-1}$), reaching sevenfold higher values under extreme acidification ($10 \pm 3 \text{ g m}^{-2} \text{ yr}^{-1}$). Stable isotopes suggest that these patterns reflect changes in the relative contribution of seagrass, macroalgae, and epiphytes to buried carbon. These findings reveal that ocean acidification can substantially alter coastal carbon cycling, potentially through shifts in community composition, with important implications for understanding past and future feedbacks between seagrass ecosystems and the marine carbon cycle.

Introduction

Seagrass meadows are hotspots for organic carbon (OC) burial and their conservation and restoration are proposed as potential nature-based solutions for climate change mitigation^{1,2}. Seagrasses, their associated epiphytes, and macroalgae fix CO₂ in their tissues through primary production, a part of which is buried in the underlying sediments. In addition, their physical influence on water flow facilitates the settling of suspended particles imported from adjacent systems, contributing to additional OC burial³. Due to anoxic sediment conditions and the stabilizing effect of a seagrass meadow on sediments, OC buried below the sediment mixed layer can be considered sequestered on climatically-relevant timescales (>100 years)⁴. This long-term storage supports net zero CO₂ emission goals^{5,6} and further enhances the imperative for conserving and restoring seagrass ecosystems.

Seagrass ecosystems are also sources of inorganic carbon (IC), with calcifying organisms including epiphytes and macroinvertebrates⁷⁻⁹ contributing to calcium carbonate (CaCO₃) precipitation and burial. However, calcification is often neglected in blue carbon studies^{10,11}, despite the fact that calcification produces CO₂¹². The subsequent sediment burial of IC is thus a source of CO₂, which can partly offset or even reverse the climate benefits of OC burial¹³⁻¹⁶. The net CO₂ sequestered depends on the balance between OC and IC burial rates, assuming similar timescales of formation and preservation¹¹.

Meadows of the species *Posidonia oceanica*, endemic to the Mediterranean, are exceptionally efficient in sequestering carbon¹⁷. Estimates of *P. oceanica* OC burial range from 24 – 140 g m⁻² yr⁻¹ ref. ¹⁸⁻²¹ with the variability driven by plant traits (e.g., aboveground biomass) and geomorphological setting¹⁷. Meadows of *P. oceanica* are also considered major sources of carbonate²²⁻²⁴, estimated to bury 54 – 741 g CaCO₃ m⁻² yr⁻¹ ref. ^{25,26}. However, while studies of

current and past burial rates are essential to constrain the seagrass carbon sink potential, it is not well known how seagrass carbon sequestration will be affected by projected future decreases in seawater pH²⁷, known as ocean acidification (OA).

CO₂ vents, which decrease seawater pH locally, have been widely used as functional analogs of future OA to assess marine environmental responses to reduced pH and altered carbonate chemistry²⁸⁻³⁰. The seawater surrounding these vents exhibit large, short-term (hours) temporal pH variability, partly because of variable hydrodynamics and local biotic feedbacks (e.g., primary production, respiration, and calcification). Moreover, the addition of dissolved inorganic carbon (DIC) from the vents reduces the buffering capacity of seawater, which inherently increases the variability of the carbonate system and lowers the calcium carbonate saturation state (Ω)^{31,32}.

Seagrass primary production has previously been observed to be DIC-limited and their photosynthesis may therefore increase with enrichment in seawater DIC associated with OA³³⁻³⁵. Together with reduced light-competition with calcareous epiphytes⁹, this can result in elevated seagrass productivity under OA conditions. For instance, seagrass community productivity was nearly twice as high at CO₂ vent sites compared to off-vent sites in Papua New Guinea³⁶. This increased productivity corresponded to higher seagrass cover and biomass of multiple seagrass species³⁷, with similar observations reported from CO₂ vents in Ischia, Italy^{28,38}. However, recent studies have not been able to reproduce this OA stimulation in the laboratory^{39,40}, and the literature is equivocal with regards to the effect of OA on seagrass community production. The discrepancy most likely depends on the level of biological organization studied (e.g., organisms/community) and the timescale of experiments (e.g., days/weeks). In addition, other phototrophic members of a seagrass meadow community (e.g., epiphytes, macroalgae) also

respond to changes in seawater pH. Because these groups can differ substantially in the direction and magnitude of their pH responses, altered pH conditions may favor some taxa while disadvantaging others, leading to indirect changes in community structure and/or community productivity. Consequently, community-level responses to pH may vary depending on the relative contributions of these groups^{42,43}. To our knowledge, the only study assessing seagrass (*Cymodocea nodosa*) sediment carbon in relation to pH found lower sediment OC stocks with lowered pH⁴⁴. Yet, only surficial (top 2 cm) sediment was assessed and differences between pH regimes may have been confounded by other site-specific differences. Consequently, the net effect of OA on seagrass meadow community production and the resulting long-term effects on the carbon sink capacity remain unresolved.

The overarching aim of this study was to assess seagrass carbon burial across three different seawater pH regimes (ambient, low, and extreme low pH; Supplementary Table 1), to investigate: 1) the stocks and burial rates of OC and IC, and 2) the sources of sediment OC influencing these rates. Ultimately, we sought to understand whether the effect of OA can be detected in the sediment record. To achieve this, we collected 14 seagrass sediment cores in three different CO₂ vent sites in Ischia, Italy and assessed carbon burial rates, carbon stocks, and stable isotope signatures throughout each core. We used stable isotope and carbon-to-nitrogen ratio (C:N) data of the dominant primary producer groups (*P. oceanica*, epiphytes, and macroalgae) at the sites to evaluate their respective contribution to sediment OC.

We found that OC burial increased substantially as pH declined, and stable isotope data indicated that these changes stem from a shift in the dominant sources of organic matter being buried. However, inorganic carbon burial offset much of the CO₂ uptake at ambient pH, leaving only the most acidified meadows as true CO₂ sinks.

Results

Variability in sediment core profiles

Out of the 14 cores analyzed, eight could be reliably dated and allow for a robust estimation of burial rates and stocks in recent decades (Supplementary Table 1). These dated cores revealed that sediment accretion rates (SAR) were highly variable between cores and ranged between 0.9 and 5.4 mm yr⁻¹, averaging 2.8 ± 1.9 mm yr⁻¹ (mean $\pm$ SD, n = 8 cores), with no clear effect of pH regime on SAR. The maximum age in the deepest section of dated sediments that could be calculated for these cores ranged from 69 to 120 years, averaging 80 ± 16 years. To compare differences between pH regimes, cores were standardized to their common estimated oldest date, which was the year 1954.

The effect of pH regime on carbon stocks and burial rates

OC burial rates increased strongly with decreasing pH, with annual rates of 1.5 ± 0.5 , 7 ± 1 , and 10 ± 3 g m⁻² yr⁻¹ (mean $\pm$ SE) between the years 1954 to 2021 at ambient, low, and extreme low pH sites, respectively (Fig. 1). Generalized least squares modeling indicated that low ($\beta = 2.92$, $p = 0.0001$) and extreme low pH ($\beta = 4.86$, $p = 0.0002$) conditions significantly increased burial relative to ambient conditions, while water depth had a smaller but significant negative effect ($\beta = -0.49$, $p = 0.0002$; Supplementary Table 2). ANOVA results confirmed that pH regime was the strongest predictor of burial rate ($F_{2,165} = 46.7$, $p < 0.0001$), followed by water depth ($F_{1,165} = 10.6$, $p = 0.0014$). Correspondingly, the OC stocks accumulated since 1954 increased with

decreasing pH, averaging $52 \pm 33 \text{ g m}^{-2}$ in ambient sites, followed by $211 \pm 64 \text{ g m}^{-2}$ in low pH sites, and $398 \pm 148 \text{ g m}^{-2}$ in extreme low sites (Fig. 1). Integrated over the top $20 (\pm 0.6) \text{ cm}$, OC stocks ranged from 86 g m^{-2} in ambient pH sites to 420 and 695 g m^{-2} in low and extreme low pH sites, respectively. To account for potential differences in the depth of active remineralization, we also compared OC stocks (g m^{-2}) at the deepest sediment layers (typically below 15 cm) where OC contents were stable with depth. The same increasing trends with lower pH were observed here, with an average of $24 \pm 5 \text{ g m}^{-2}$ at ambient pH, $41 \pm 11 \text{ g m}^{-2}$ at low pH, and $60 \pm 54 \text{ g m}^{-2}$ at extreme low pH.

The estimated IC stocks and burial rates were relatively similar between pH regimes during the period 1954-2021 (Supplementary Figure 1), with no factor explaining differences better than the null model (Supplementary Table 3). Consequently, the molar ratio of organic to inorganic carbon content (OC:IC) increased with lower pH, averaging 0.13 ± 0.07 , 0.44 ± 0.10 , and 0.84 ± 0.21 in ambient, low pH, and extreme low pH sites, respectively during this period. The relationship between OC and IC became even stronger when also including older sediment fractions and non-dated cores (Fig. 2b). As such, OC burial is driving the higher OC:IC ratios at these sites. Due to the overall low OC:IC ratios (0.49 ± 0.44), the *P. oceanica* meadows were on average a net source of CO_2 to the atmosphere (Fig. 2c). Notably, the only cores that on average provided net sequestration of CO_2 during these past ~70 years were found in extreme low pH regimes.

The effect of pH regime on stable isotope signatures and C:N ratios

The prevailing pH regime also influenced the stable isotope signatures of the buried organic matter. There appeared to be a weak, albeit not significant (ANOVA; $F_{2,5} = 0.23$; $p = 0.80$) trend of decreasing sediment $\delta^{13}\text{C}$ with decreasing pH where the signature of $\delta^{13}\text{C}$ exhibited marginally more depleted values (mean $\pm$ SE) in low pH (-18.94 ± 0.58 ‰), and extreme low pH sites (-18.82 ± 0.86 ‰) relative to ambient pH sites (-18.07 ± 1.05 ‰). The signature of $\delta^{15}\text{N}$ revealed a non-linear trend ($F_{2,5} = 6.9$; $p = 0.04$), with highest values in low pH sites (5.13 ± 0.41 ‰) and similar between ambient pH sites and extreme low pH sites (4.26 ± 1.52 ‰ and 4.07 ± 0.62 ‰, respectively). The average sediment C:N ratio during 1954 – 2021 ranged from 13.3 ± 2.3 in ambient pH sites to 21.2 ± 2.4 in low pH sites and 24.6 ± 3.6 in extreme low pH sites (Fig. 3). However, the trends are not clear in endmember C:N ratios but display a substantially higher overall ratio in *P. oceanica* compared to epiphytes and macroalgae (Fig. 3c). Tissues of *P. oceanica* exhibited higher $\delta^{13}\text{C}$ compared to macroalgae and epiphytes irrespective of pH regime (Fig. 3a), but displayed a pH-dependent relative magnitude in $\delta^{15}\text{N}$ (Fig. 3b).

The isotope mixing model revealed a change in endmember contribution between pH regimes (Fig. 4). In ambient pH sites, model results indicated that *P. oceanica* (80 ± 5 %) was the most important source to sediment organic matter ($P = 100$ %), followed by epiphytic algae (12 ± 7 %) and macroalgae (8 ± 5 %). In low pH sites ($P = 99$ %), *P. oceanica* contributed less (62 ± 6 %), followed by macroalgae (25 ± 4 %) and epiphytic algae (13 ± 9 %). In extreme low pH sites ($P = 67$ %), the contribution of seagrass was even lower (45 ± 12 %), slightly less by epiphytic algae (33 ± 20 %) and other macroalgal species (22 ± 9 %). However, these trends were not reproduced for the most recent time period (1954 – 2021, Fig. 4d-e). Here, *P. oceanica*

contributed most at ambient pH (55 ± 12 %; $P = 81$ %), but with no apparent difference between low pH (45 ± 9 %) and extreme low pH (42 ± 14 %).

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Discussion

Stocks and burial rates in recent times

The average (mean $\pm$ SE) OC burial rates for the period 1954 – 2021 reported herein ($1.5 - 10 \text{ g m}^{-2} \text{ yr}^{-1}$) fall below the global mean for seagrass meadows ($26 \pm 3 \text{ g m}^{-2} \text{ yr}^{-1}$)⁴⁵ and are also lower than rates in nearby areas such as the Balearic islands, Spain ($26 \pm 6 \text{ g m}^{-2} \text{ yr}^{-1}$)²⁰, Greece ($34 \pm 24 \text{ g m}^{-2} \text{ yr}^{-1}$)²⁶, Sicily, Italy ($24 \pm 4 \text{ g m}^{-2} \text{ yr}^{-1}$)²¹. Similarly, IC burial rates in Ischia ($13 \pm 1 - 26 \pm 2 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) are about an order of magnitude lower than the average global rates for seagrass ($182 \pm 94 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)¹⁴ and considerably lower than a recent estimate from the past 500 years in *P. oceanica* meadows in Greece ($405 \pm 336 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)²⁶. As such, the meadows in Ischia do not represent hotspots for carbon burial. While substantial differences in sediment depth and timescales of integration complicate comparisons across studies, our findings consistently show that burial rates are relatively low in Ischia.

The seagrass meadows in Ischia exhibited large variability in SAR ($0.9 - 5.4 \text{ mm yr}^{-1}$), with rates similar to recently reported SAR in *P. oceanica* meadows in Greece ($0.5 - 4.1 \text{ mm yr}^{-1}$)²⁶ and the Balearic islands ($2.4 - 4.2 \text{ mm yr}^{-1}$)¹⁸. This indicates that, despite spatial heterogeneity, sedimentation dynamics are not the primary factor underlying the low carbon burial rates observed in Ischia.

Seagrass organic carbon burial as a function of pH regime

We found an increase in OC burial rates as a function of decreased pH, that appeared to be directly driven by higher carbon fixation. The observed differences in OC burial between pH regimes could be due to several direct and indirect effects, which we discuss below.

First, sediment OC underlying *P. oceanica* meadows is largely autochthonous¹⁷ (Fig. 4), and several laboratory studies have shown that net primary production is stimulated by a lowered pH due to increased CO₂-availability⁴⁶⁻⁴⁹. The higher OC burial rates observed at low pH may therefore be a result of elevated primary production, yielding more fixed carbon available for burial. However, the net effect of a consistently lowered pH on *P. oceanica* community productivity remains largely unresolved, with contrasting evidence in the literature. There are *in situ* and mesocosm studies reporting increases⁴⁷, decreases⁴⁰ and no apparent effects⁴⁹⁻⁵² in response to low pH. The net effect of community productivity is modulated by the individual response of each community constituent (e.g., *P. oceanica*, epiphytes, macroalgae, invertebrates), which can influence each other through biotic interactions. For instance, it has been shown that the epiphytic community on *P. oceanica* leaves in Ischia is the largest contributor to net primary productivity (NPP) when exposed to ambient pH but contributes a lower proportion of NPP at lowered pH⁴⁸. This was attributed to both a direct stimulation by higher CO₂ availability and indirectly through released light-competition with calcareous epiphytes that were less abundant at vent sites⁴⁸. In contrast, our results indicate that the combined contribution of calcifying and non-calcifying epiphytes to sediment OC increased at lower pH (Fig. 4), although the relative contribution of the two forms could not be determined. Furthermore, it is possible that allochthonous inputs of epiphyte-derived IC contribute to our contrasting results, as acidification at these sites is highly localized.

Second, any reduction in remineralization rates of sediment OC will manifest as increased OC burial rates. Exposure to low seawater pH can alter the composition of detritivore and meiofaunal communities^{53,54}, as well as the microbial abundance in the sediment⁵⁵, with implications for OC remineralization. It is thus plausible that low pH-induced decreases in the

efficiency of OC decomposition are driving the differences in OC stocks and burial rates observed across pH regimes. To minimize the potential influence of this factor, we also compared the OC content at sediment depths (typically below 15 cm) where the OC content was constant with depth, i.e., where remineralization is negligible¹³. This analysis corroborated the trend of the overall OC burial rates, with 30- and 40-fold increases in low pH and extreme low pH, respectively, relative to ambient pH. As such, it is unlikely that differences in OC burial rates between pH regimes are due to changes in the rate of remineralization. In fact, studies on long-term acidification in CO₂ vent sites have found organic matter decomposition increases with a lowering of pH^{53,54}. For instance, water column decomposition rates of the refractory detrital pool were 40 to 67 % higher at low pH relative to ambient pH, likely driven by an observed increase in detritivore abundance at acidified conditions⁵³. Moreover, meiobenthic communities exhibited a significantly altered species composition at vent sites in Ischia, relative to ambient pH⁵⁴. Herbivory on *P. oceanica* has also been reported to be higher at vent sites relative to ambient pH^{56,57}. Collectively, these studies suggest that remineralization would be higher at acidified conditions resulting in a lower OC burial rate, thus contrasting with our findings.

Third, localized acidification can shift the benthic community composition, altering the relative abundance of seagrass, macroalgae and other epiphytes⁵⁸ – key sources (endmembers) of sediment OC. These shifts may influence net community productivity through complementarity effects^{59,60}. For instance, structurally complex canopies with a higher phototrophic diversity can enhance light-use efficiency⁶¹ due to mechanisms such as self-shading, pigment complementarity, or varied photosynthetic pathways (e.g., C3, C4, and carbon-concentrating mechanisms, CCM)⁶²⁻⁶⁴. We observed a distinct shift in endmember contributions at vent sites, with epiphytes and macroalgae having an increased influence on OC buried relative to *P.*

oceanica (Fig. 4), consistent with a change in macrophyte community composition. Importantly, the negative effect of water depth on OC burial could reflect a difference in light availability that also influences community composition and productivity. Nevertheless, whether changes in community composition affects OC burial in response to OA should be a focal point in future research. To improve the endmember attribution to sediment OC burial, future studies should expand the proxies used, possibly including biomarkers, combine sediment assessments with benthic surveys of species composition, and constrain advective fluxes of allochthonous organic matter.

The role of inorganic carbon and the effect on net CO₂ sequestration

Calcium carbonate production and burial have received comparatively little attention in the blue carbon literature despite its relevance for carbon budgets and climate change mitigation potential^{11,13}. The OC:IC ratio in ambient pH sites (0.30) falls close to the median seagrass ratio of 0.20 previously reported⁶⁵, whereas acidified sites exhibited much higher ratios at low pH (1.01) and nearly twice as much OC compared to IC in extreme low pH (OC:IC = 1.92). As such, incorporating IC burial as an offset to CO₂ sequestration renders the seagrass meadows in ambient pH sites sources of CO₂, near neutral but highly variable in low pH sites, and sinks of CO₂ only in extreme low pH sites (Fig. 3). Despite large variability between cores, the lowered pH appears to simultaneously increase sediment OC content and decrease IC content (Fig. 3), possibly due to a concurrent stimulation of net community production (NCP) and reduction of net community calcification (NCC). Similar findings have been reported for seagrass meadows (*Halodule* spp.) in Brazil¹⁵, where the inclusion of IC in carbon burial estimates resulted in the meadows being a net source, releasing $6340 \pm 66800 \text{ g CO}_2\text{eq m}^{-2}$, albeit with substantial

variability. Notably, because seawater buffering capacity decreases with declining pH, the ratio of released CO₂ to precipitated carbonate is expected to increase relative to present-day conditions¹² resulting in an even larger offset to the seagrass OC burial with future OA¹³.

In a Florida Bay seagrass meadow, it was found that CO₂ emissions from calcification and subsequent IC burial far exceeded CO₂ uptake via OC burial, resulting in a net source of CO₂ to the atmosphere of 268 g CO₂eq m⁻² yr⁻¹¹⁶. A recent meta-analysis of 15 seagrass studies highlighted that although seagrass meadows exhibited substantial IC burial rates (182 ± 94 g m⁻² yr⁻¹), much of the calcification occurred in adjacent ecosystems and was imported through lateral fluxes¹⁴. As a result, most IC deposited in these meadows was considered allochthonous and did not counterbalance OC burial¹⁴. Nevertheless, nearly 95% of the CO₂ flux from the sea to the atmosphere in the Florida Bay meadow was attributed to autochthonous IC production¹⁶. While the assertion by Saderne et al¹⁴ that most IC is allochthonous likely holds true for many carbonate-poor meadows, the prevailing assumption in many blue carbon studies is that all buried OC is either a direct (autochthonous OC) or indirect (allochthonous OC) effect of the seagrass, and blue carbon studies rarely account for allochthonous import of OC that would have occurred in the absence of the seagrass⁶⁶. Consequently, OC burial rates are typically not differentiated by provenance, despite introducing the risk of counting OC sequestration twice, which has considerable implications for carbon accounting and carbon credits assessments⁶⁷.

In conclusion, we report elevated OC burial in response to OA that appears to be linked to a shift in seagrass meadow community composition characterized by a relative increase in epiphytes and macroalgae. However, high rates of autochthonous calcification may offset any climate benefits under contemporary and near future pH scenarios. The apparent positive effect of OA on net CO₂ sequestration reported herein highlights the potential for a feedback process

that can strengthen the CO₂ sink potential of these meadows in the future. At the same time, our findings also underscore the importance of management actions that minimize source behavior in sites with high calcification or net CO₂ release, highlighting that both enhancing sinks and reducing sources are integral to effective mitigation strategies and climate accounting.

Methods

Study area

Ischia is a volcanic island in the Tyrrhenian Sea, Italy. CO₂ vents occur predominantly on the south-eastern side of the island, spanning depths from 0.5 to 48 m^{68,69}. These vents release gas containing 90.1 – 95.3 % CO₂, with no sulfur or effects on seawater temperature or salinity^{28,69}. As such, the CO₂ released creates localized seawater acidification and increase in the variability of the seawater carbonate system that can be attributed to CO₂ input, rather than to coincident changes in other abiotic factors²⁹. Seagrass sediment cores (n = 14) were sampled across three distinct pH regimes including ‘Ambient pH’ (pH_T, pH on the total scale $\approx$ 8.0 – 8.1; $p\text{CO}_2 \approx 440 \mu\text{atm}$) representing present-day conditions, ‘Low pH’ (pH_T = 7.8 ± 0.31 ; $p\text{CO}_2 \approx 1580 \mu\text{atm}$) representing the expected surface pH_T at the end of this century under the RCP8.5 scenario^{70,71} and ‘Extreme low pH’ (pH_T $\approx$ 6.6 – 7.2; $p\text{CO}_2 \approx 24000 \mu\text{atm}$) representing a more distant future or extreme scenarios^{30,72}. See Supplementary Table 1 for a detailed description of sediment cores, sites, and pH conditions. The pH regimes were established in a previous study^{53,69,73}, using *in situ* pH sensors (SeaFET, Honeywell Inc.) recording pH_T at 1h and 15-minute intervals. For a detailed description of sensor deployments, calibration and data, refer to Teixidó, et al. ⁶⁹.

We collected seagrass sediment cores and macroalgal tissues at three sites spanning water depths from 1.5 to 12.3 m, comprising CO₂ vents and reference areas with no venting activity

and ambient pH (Supplementary Figure 2). The site Castello Sud ($n = 4$ cores) is located along the rocky coast of Castello Aragonese where CO₂ gas bubbles emerge from the seafloor at 0.5 to 3 m depth. Cores ($n = 2$) were collected 20 m from the islet's southwestern shore at shallow depths, where CO₂ bubble emissions indicate vent activity. A *P. oceanica* meadow is found directly within the bubbling zone, extending outward along the gradient of decreasing $p\text{CO}_2$. Two additional reference cores ($n = 2$) were collected at the end of the gradient where $p\text{H}_\text{T}$ is ambient. The Vullatura site ($n = 6$ cores) is situated approximately 180 m from the northeastern coast of Ischia. The CO₂ vent zone spans approximately 30–40 m, characterized by intense visible bubbling in a 'caldera', occurring at depths of 4–6 m. A *P. oceanica* patch is present within the caldera, adjacent to a larger *P. oceanica* meadow⁵³. The ambient pH zone was established approximately 200 m away from the caldera at 5.4 m depth, with no visible venting activity and used as reference area⁵³. In Chiane del Lume, sediment cores ($n = 4$) were collected, at depths between 11 and 12 m. Similar to Vullatura, most active bubbling occurs within the gravelly substrate of the caldera. *Posidonia oceanica* meadows occur within and beyond the vent area.

The exact onset of vent activity is uncertain. At Castello Aragonese, CO₂ bubbling has likely occurred for centuries, with modest activity noted in the 1970s–1980s and a clear intensification over the past two decades⁶⁸. We followed the established three-zone pH classification used in previous studies^{29,30,68}, although the venting area has expanded in the past decade. For Vullatura and Chiane del Lume, we applied the zoning defined by Lee et al.⁵³ and Teixidó et al.⁶⁹; these vents were first documented recently but likely began emitting CO₂ earlier as part of the same volcanic system.

Field sampling

The field study was conducted between 7 and 11 June, 2021. We collected 14 sediment cores (Supplementary Table 1) via SCUBA using PVC cylinders (ID = 6.3 cm; length = 100 cm) that were hammered into the sediment using a rubber sledge. The insertion depth was noted and each core carefully extracted from the sediment, plugged and taped in both ends and transported to the laboratory in a vertical position. Compaction (49 ± 21 %) during sampling was assessed by measuring the depth to the sediment surface inside and outside of the core (Supplementary Table 1). A correction factor was calculated for each core to correct the thickness of sediment layers prior to depth-based stock estimates, assuming linear sediment compaction along the core¹⁸.

Macroalgae present in the seagrass meadows were sampled in Castello and Chiane del Lume, covering ambient, low pH, and extreme pH sites. Organic tissue carbon and nitrogen isotope values were obtained for macroalgal samples ($n = 4$ to 7 individuals for each species across each pH regime).

Sediment core processing

Each core was cut horizontally, the length of the core measured, and the sediment composition and any visible features (e.g., color, root fragments) qualitatively assessed. Cores were sliced at 0.5-cm intervals down to 20 cm, and the remaining core at 1-cm intervals. Slices were dried and any visible root fragments removed to obtain sediment dry mass (g) and use for elemental and isotope analyses.

Elemental and stable isotope analyses

Sediment total carbon (TC), total nitrogen (TN), and stable isotopes of ^{13}C and ^{15}N were measured using an elemental analyzer (Costech 4010) coupled to an isotope-ratio mass spectrophotometer (IRMS, Thermo-Finnegan Delta V) at the University of Hawai'i at Hilo, USA. To obtain OC and ^{13}C -OC, subsamples of dried sediment slices were acidified (4 % HCl) to remove IC. After acidification, the sample was centrifuged and the supernatant discarded using a pipette. Samples were washed with Milli-Q, centrifuged and the supernatant discarded one more time. The samples were then dried, encapsulated in tin and analyzed by the elemental analyzer. Stable isotope data are reported as $\delta^{13}\text{C}$ relative to Vienna Pee Dee Belemnite and $\delta^{15}\text{N}$ relative to air. The quality of isotope measurements was controlled using certified reference material (Buffalo River Sediment, NIST8704). The fraction of IC was estimated based on the mass loss due to sample acidification, assuming that all CaCO_3 was dissolved, and that IC makes up 12% of CaCO_3 mass lost according to that the molar mass of $\text{CaCO}_3 = 100.086 \text{ g mol}^{-1}$ and the molar mass of C = $12.011 \text{ g mol}^{-1}$.

Macroalgal samples were cleaned of inorganic material and epiphytes with de-ionized water and tweezers, dried and ground into a fine powder using an agate mortar and pestle. Stable isotope analyses were conducted on ground samples using a DELTA V Plus continuous flow IRMS linked to a Flash 2000 elemental analyzer using a MAS 200 R autosampler (Thermo-Fisher Scientific) at the New Zealand Institute for Earth Sciences Ltd. in Wellington, New Zealand. International reference materials were used to determine isotopic values following Paul et al⁷⁴. Carbon isotopic values were reported as $\delta^{13}\text{C}$ and two-point normalized from daily analysis of certified standards (NIST 8573 & L-Valine #2), with an accuracy and precision of $0.11 \pm 0.05 \text{ ‰}$. Nitrogen isotopic values were reported as $\delta^{15}\text{N}$ relative to atmospheric air and corrected against certified standards (NIST 8573 & NIST 8548). Accuracy and precision ($0.20 \pm$

0.14 ‰) were determined by the repeat analysis of certified standards and the working laboratory internal standard DL-Leucine, respectively.

Radionuclide analyses

Sediment cores were analyzed for ^{210}Pb to determine the sediment accumulation rates. The concentrations of ^{210}Pb were determined by alpha spectrometry via measurement of its decay product ^{210}Po after digestion in acid media using an analytical microwave in presence of ^{209}Po as an internal tracer and plating onto silver disks⁷⁵. Excess ^{210}Pb concentrations were determined as the difference between total ^{210}Pb and ^{226}Ra (supported ^{210}Pb), the latter analyzed by gamma spectrometry at various depths along each core. The concentrations of ^{226}Ra were quantified via the emission peaks of its two decay products ^{214}Pb (295 and 352 keV) and ^{214}Bi (609 keV) using a high-purity germanium detector (CANBERRA, mod. GCW3523) in calibrated geometries after equilibrium between ^{226}Ra and its progeny had been reached (21 days).

Age-depth model, sedimentation rates and carbon burial rates

Sediment accumulation rates were estimated, where possible, by applying the CF:CS (Constant flux:Constant sedimentation^{76,77}) model to the excess ^{210}Pb concentration profiles, which allows obtaining the mean mass accumulation rate (MAR, $\text{g cm}^{-2} \text{ yr}^{-1}$) and SAR (mm yr^{-1}). In cases where a mixed layer was identified (Supplementary Figure 3), MAR was calculated below it. Out of the 14 cores analyzed, ten cores could be dated, of which eight cores had a shallow enough mixed layer to cover recent decades (1954-2021; Table S1).

Sediment content (% dry weight) of OC and IC were converted to carbon mass (g cm^{-2}) by multiplying the content by sediment mass (g) and dividing by the core surface area (cm^2).

Stocks of OC and IC were then computed as the cumulative mass along each core down to the year 1954. For stocks standardized to fixed sediment depth, the compaction-corrected depth was used. Carbon burial rates were computed as the mass-weighted average content of organic or inorganic carbon, multiplied by MAR.

The subset of eight cores dated between 1954-2021 was used for all comparisons of OC and IC burial and stocks between pH regimes unless otherwise stated.

Comparing differences between pH regimes

To compare differences between pH regimes cores for which an age-model could be obtained, cores were standardized to their common estimated oldest date, which was the year 1954. Group means of each pH regime (ambient, low pH, and extreme low pH) were computed using core averages within each group along with the propagated standard error of each group mean (SE).

We used linear mixed effects models (package *lme4*⁷⁸) and generalized least squares (GLS) models (package *nmle*⁷⁹) to evaluate differences in OC and IC stocks and burial rates, C:N and OC:IC molar ratios, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures across pH regimes, sites and water depths. Core ID was included as a random intercept in the models to account for repeated measurements within cores and to avoid pseudo-replication. Assumptions of models were evaluated (package *DHARMA*⁸⁰) and response variables were square root transformed to fulfill the normality assumption when necessary (OC:IC ratio). For response variables derived from the subset of dated cores in the period 1954-2021 (OC and IC stocks and burial rates), residual variances were heterogeneous and representation across pH regimes was unbalanced, with only one Ambient core compared to multiple low-pH cores (Supplementary Table 1). We therefore used GLS models with group-specific residual variances to accommodate both heteroscedasticity and the

unequal sampling structure, preventing the single Ambient core from being overly influential. Competing models were evaluated based on corrected Akaike Information Criterion (AICc) and likelihood ratio tests (package *MuMIn*⁸¹) and the best model for each response variable was selected (Supplementary Table 3). Significance ($p < 0.05$) of fixed effects was evaluated via Type III ANOVAs. Pairwise differences among pH regimes were tested using Tukey's post hoc test (package *emmeans*⁸²). All analyses were carried out in R version 4.4.1⁸³.

We used the burial rates ($\text{g m}^{-2} \text{yr}^{-1}$) of organic carbon (R_{OC}) and inorganic carbon (R_{IC}) to compute the net CO_2 flux, assuming a ratio of released CO_2 to precipitated calcium carbonate (Ψ) of 0.6¹², as:

$$\text{CO}_2 \text{ flux } (\text{g CO}_2\text{eq m}^{-2}\text{yr}^{-1}) = (R_{OC} - R_{IC} \times \Psi) \times \frac{44.01}{12.01} \quad (1)$$

Because Ψ is expected to increase with decreasing pH¹², the use of a constant Ψ likely yields conservative estimates of CO_2 fluxes under acidified conditions. The estimated flux was converted to CO_2 equivalents (CO_2eq) using the molecular weight ratio of CO_2 to C.

Stable isotope mixing model

The isotopic signature of bulk sediment OM reflects the relative contribution of endmembers, together with post-depositional processes conducive to isotopic fractionation. As such, differences in endmember importance can be compared among pH regimes. We used the signature of stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to study the contribution of dominant sources of organic matter to the sediment. Data from previous studies of Ischia phototrophs sampled across the three pH regimes were used together with our macroalgal data to obtain pH specific input values. To compare differences in endmember contributions across pH regimes, endmembers were combined into three distinct groups (Supplementary Table 4): 1) '*P. oceanica*', 2)

‘Macroalgae’, mainly comprised of large algae species of the genus *Dictyota* spp., *Caulerpa* spp., *Halopteris* spp., and *Flabellia* spp. and 3) ‘Epiphytes’, consisting of erect epiphytic filamentous algae found on *P. oceanica* leaves (Supplementary Table 4). We applied a Bayesian mixing model (package *simmr*⁸⁴) using Markov chain Monte Carlo (MCMC) sampling with four parallel chains with 3600 iterations in total. The first 450 iterations of each chain were discarded as burn-in, leaving approximately 1800 posterior samples for inference. Convergence was evaluated using Gelman–Rubin diagnostics ($\hat{R}$) and trace plots, with all parameters showing good mixing and $\hat{R}$ values < 1.1 . Differences in endmember contributions were inferred from their posterior probability (P). It is inherently difficult to separate macroalgae from phytoplankton and seston as these share similar isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) on group level^{85,86}, and because phytoplankton and seston move across multiple pH conditions through hydrodynamics, these groups were excluded from the model. In addition to stable isotopes, we obtained literature values of C:N ratios of these groups and used the sediment C:N ratio in tandem with the isotope mixing model output to interpret the relative contribution of each endmember as a function of pH regime.

Endmember $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N ratios differed among pH regimes (Supplementary Table 4). This complicated the use of these tracers in the mixing model formulation as the pH trends of the endmembers and sediment mixture diverge. To partly overcome this, we used the average isotopic signature of all pH regimes when comparing endmember contribution among pH regimes.

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Author contributions

T.K, N.T, S.C, J-P.G, and P.M conceived the study; N.T, A.M, and S.C collected samples; B.G, S.A, I.K, D.B, C.C, and P.M analyzed samples. T.K and P.M analyzed data. T.K. wrote the manuscript with input from all co-authors.

Competing interests

The authors declare no competing interests. C.C is an Editorial Board Member for Communications Earth & Environment, but was not involved in the editorial review of, nor the decision to publish this article.

Data availability

Data are publicly available in the Zenodo repository⁸⁷ and the R script used to analyze data and produce figures is available at GitHub (<https://github.com/dillkotte/Ischia-pH-C>).

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Figure captions

Figure 1. Average (mean $\pm$ SE) annual stocks and rates in the period 1954-2021. Organic carbon (OC) stocks (a) and burial rates (b) as a function of the seawater pH regime. Points are the arithmetic mean of each core mean ($n = 8$) and errorbars indicate the propagated uncertainty as standard error (SE). Shaded violins show the distribution of values of individual core slices.

Figure 2 Organic and inorganic carbon and the net CO₂ sequestration rate. a) Linear regression of inorganic and organic carbon mass for each pH regime ambient (blue), low pH (yellow) and extreme low pH (red) (8 cores, $n = 168$ slices); where the inset panel in b) shows the same regression but includes the entire dataset including non-dated cores (14 cores, $n = 483$ slices). Panel c) shows the net CO₂ sequestered during 1954-2021 when accounting for the balance between OC and IC burial. Points are median and error bars the interquartile range. Positive values indicate a net sequestration of CO₂ whereas negative values indicate a net source of CO₂.

Figure 3 Stable isotopes and C:N ratio of endmembers and sediment. Panels show the isotopic signatures (mean $\pm$ SE) of $\delta^{13}\text{C}$ (a, d), $\delta^{15}\text{N}$ (b, e) and molar C:N ratio (c, f) of the dominant endmembers (a-c), and bulk sediment organic matter of the dated cores during the period 1954-2021 (d-f). Values in panels a-c are composed of data from this study and literature values from the same study sites (Supplementary Table 4).

Figure 4 Contribution to sediment OM as a function of pH regime. Boxplots showing results from the Bayesian mixing model using the sediment signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as tracers and

the three endmembers *Posidonia oceanica* (a, d), Macroalgae (b,e) and Epiphytes (c,f). Boxes show the interquartile range (25th – 75th percentile) of the posterior distribution and error bars show the 95% Bayesian credible interval (BCI). Panels a-c show results from the whole dataset whereas panels d-f are based on the eight dated cores in the dataset and includes the period 1954-2021. Symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science.

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Editorial summary:

Ocean acidification can alter coastal carbon cycling by altering community composition, enhancing seagrass meadow carbon burial rates, according to analyses of seagrass sediment cores and macroalgal tissues from carbon dioxide vents around Ischia, Italy.

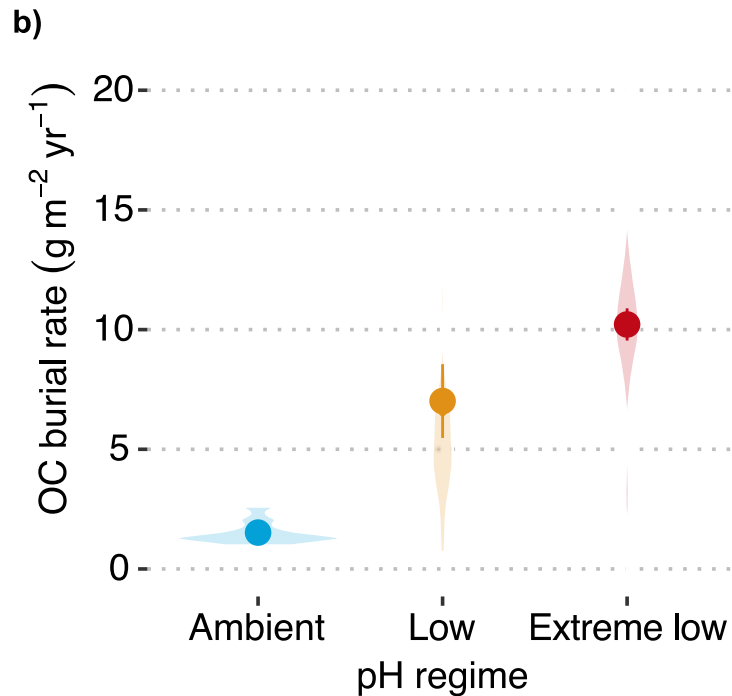
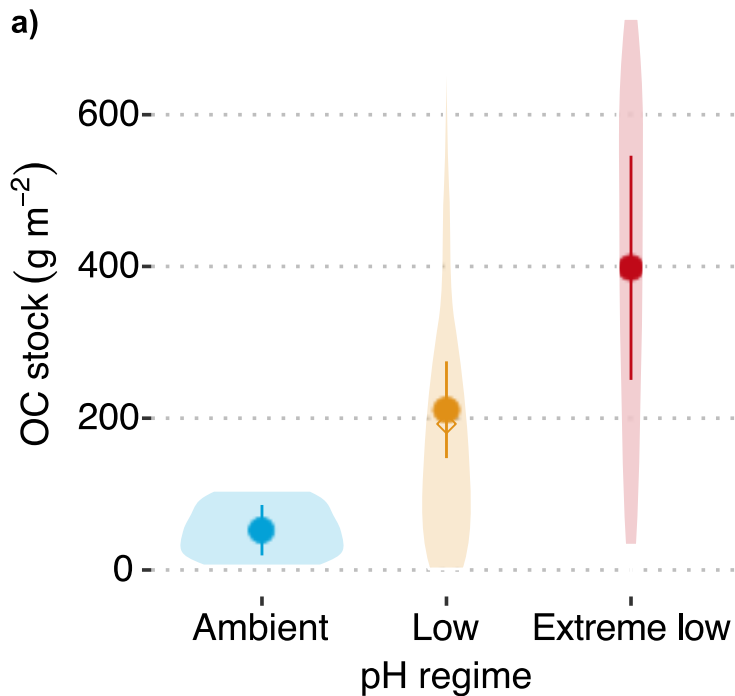
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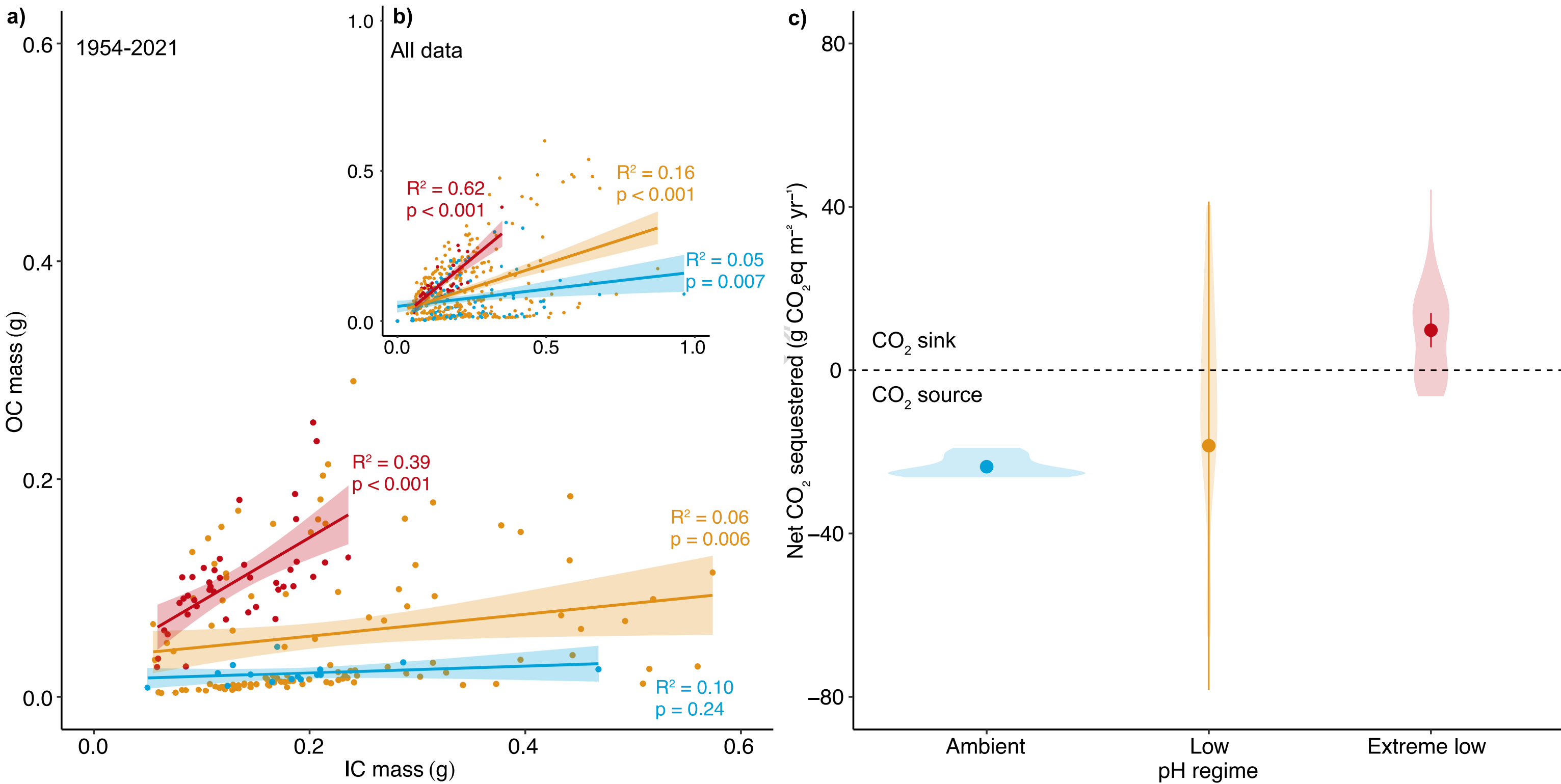
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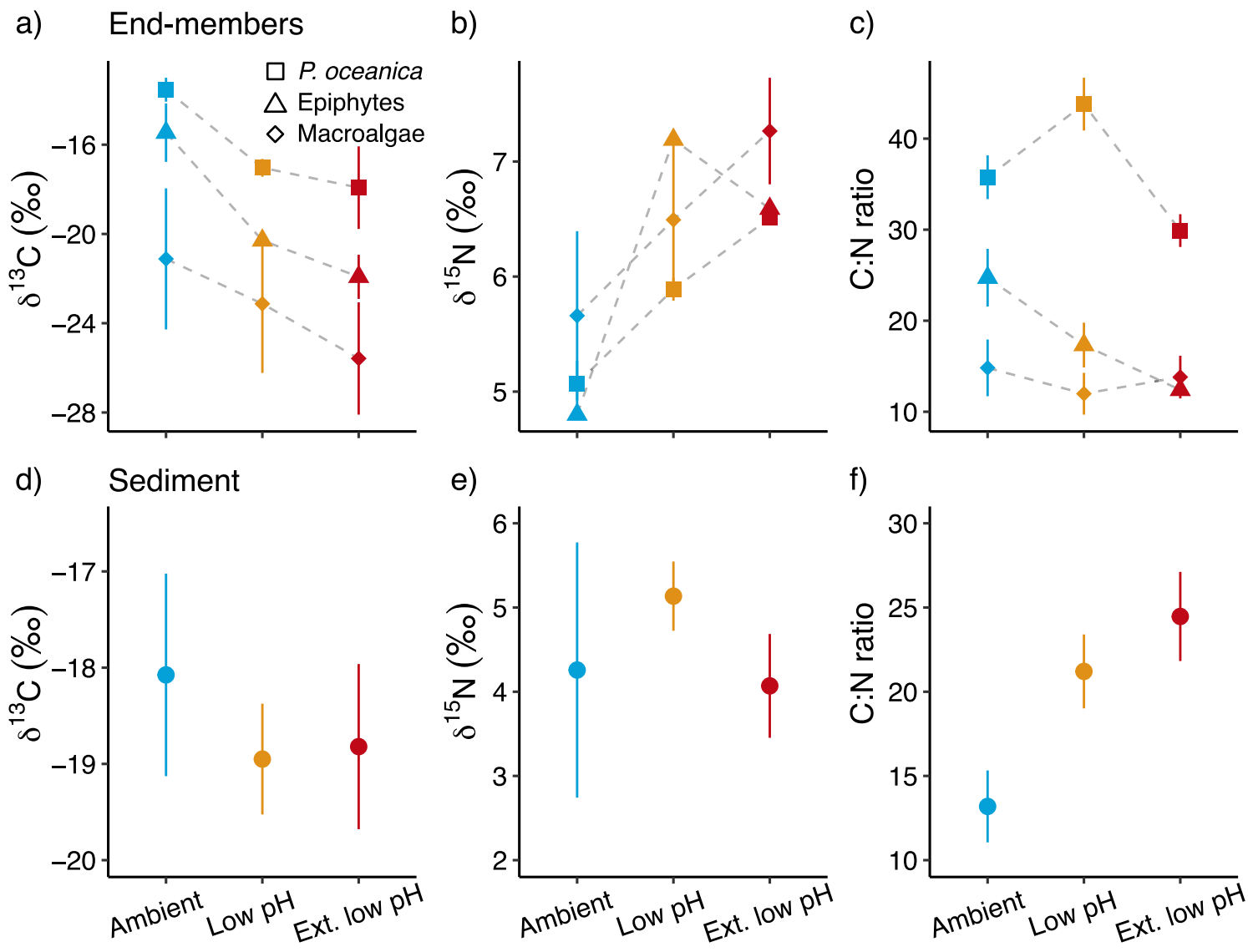
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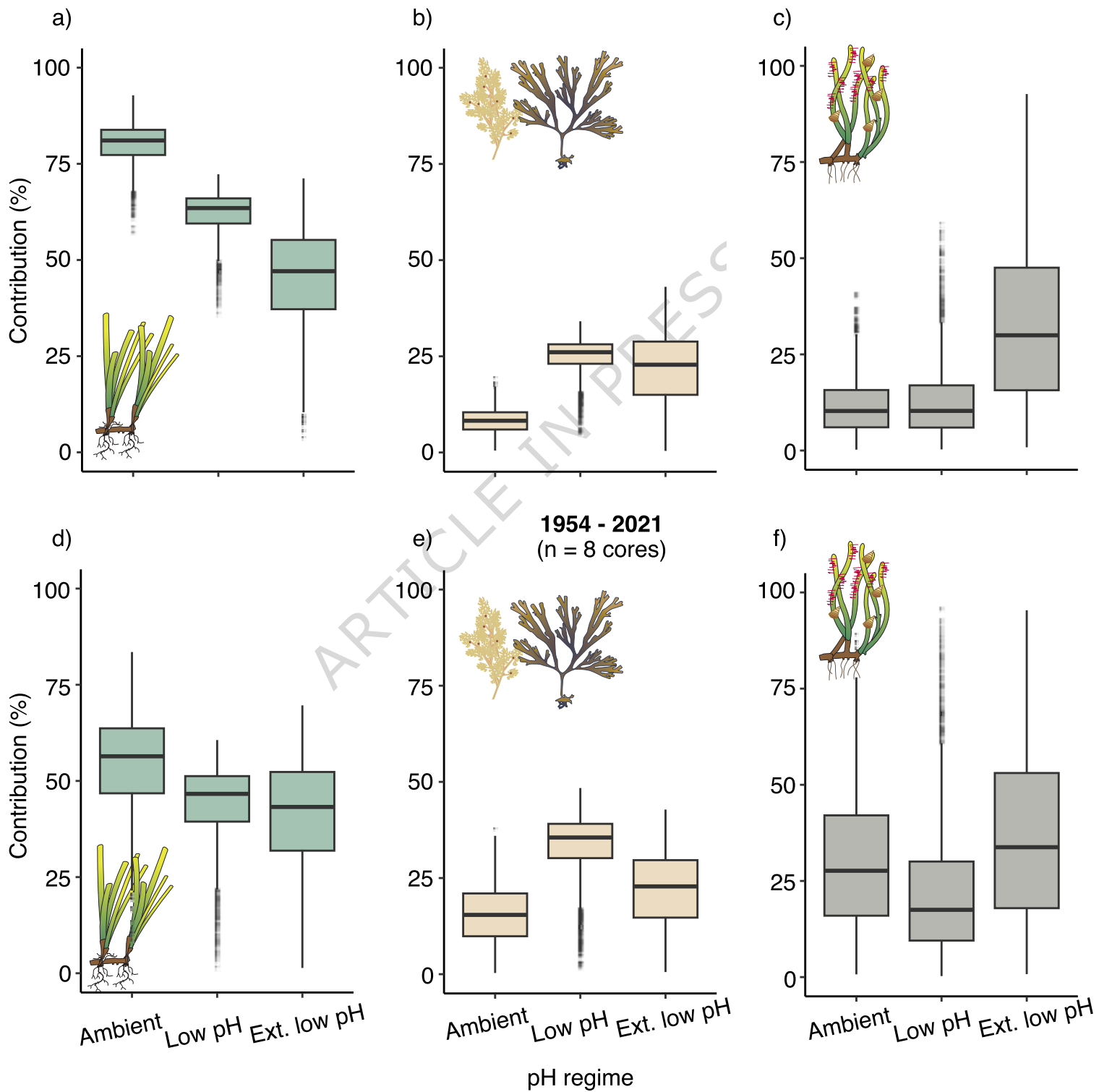
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All data
(n = 14 cores)

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