



Fiddling with the blue carbon: Fiddler crab burrows enhance CO₂ and CH₄ efflux in saltmarsh

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ABSTRACT

Saltmarshes are important global carbon (C) sinks, but the considerable uncertainty in the C budget and the underlying mechanisms limit the estimation of greenhouse gas emissions (GHG, e.g., CO₂ and CH₄) in the context of global climate change. To ascertain the mechanistic understanding, we assessed how crab burrows morphology and greenhouse gas effluxes changed in response to interactions of fiddler crab burrow density, soil organic matter content (high vs low), and presence/absence of *Spartina alterniflora* (vegetated saltmarsh vs nearby unvegetated mudflat) on the coast of New England (USA). The crab burrow volume in the vegetated saltmarsh was smaller than that in the mudflat, and crab burrow volume greatly correlated with soil CO₂ efflux, indicating that crab activities could enhance coastal wetland CO₂ efflux. Soil CO₂ and CH₄ effluxes rates were significantly positively correlated with crab burrow density, organic matter content, and vegetation types. Specifically, the higher soil organic matter content and crab burrow density greatly increased soil heterotrophic respiration in the saltmarsh. Overall, with crab disturbances, soil CO₂ and CH₄ efflux increased by 32.1% and 47.9%, respectively. This study highlights that fiddler crab burrowing activity plays an important role in the C sequestration of coastal blue C ecosystems (BCEs).

1. Introduction

Coastal wetlands, such as saltmarshes, mangrove forests, and sea-grass beds, have been increasingly considered as efficient C sinks for their high rates of C capture, high productivity, and low decomposition rates (Howard et al., 2017), referred to as coastal blue C ecosystems (BCEs) (Gedan et al., 2009; Donato et al., 2011; Wang et al., 2021). Occupying only 0.2 % of the total ocean surface, BCEs stored half of the C in marine ecosystems, accounting for 46.9 % of the C burial (Duarte

et al., 2013). In wetlands, decomposition proceeds at a slow rate due to the anaerobic conditions where, over time, moderately decomposable organic matter and the other recalcitrant fractions (Kristensen et al., 2008a; Alongi, 2014). Therefore, oxygen penetration in the sediment is key to regulating degradation processes. In coastal wetland sediment, oxygen penetration is limited by the water saturation of the sediment and the high surface oxygen demand driven by the microbial degradation of deposited organic matter, limiting the availability of oxygen in the subsurface sediment (Glud, 2008; Michaels and Ziemann, 2013).

Abbreviations: GHG, greenhouse gas emissions; BCEs, blue carbon ecosystems; LOI, loss on ignition; GLMM, generalized linear mixed model.

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However, soil-dwelling organisms create biogenic structures (e.g., burrows) that can facilitate oxygen penetration deeper into the sediment (Gribsholt et al., 2003; Kristensen et al., 2008a).

As a vital member of the intertidal ecosystem, Brachyuran crabs play an essential role in coastal wetlands as degraders, consumers, and habitat disrupters (Andretta et al., 2014; Alberti et al., 2015; Aschenbroich et al., 2016). Their bioturbation allows oxygen to penetrate deep into sediment and create an extension of the soil–air interface in coastal marshes, increasing the interchanges in the material in the intertidal zone (Smith et al., 1991; Kristensen, 2008; Thomson et al., 2020). CO₂ can be released into the atmosphere from these biogenic structures at low tide by decomposing the soil organic matter and respiration of faunal, root, and culm (Lim and Rosiah, 2007). The rate of CO₂ effluxes through carb burrows is 10,000 times faster than aqueous diffusion (Howes et al., 1985; Morris and Whiting, 1986; De la Iglesia et al., 1994). Eventually, the buried organic matter is oxidized, and the CO₂ effluxes increase by 70 % (Gribsholt et al., 2003; Otani et al., 2010; Ouyang et al., 2017). The bioturbation activities of crabs have been proven to increase the export of CO₂ and dissolved organic C in North and South American saltmarshes, reducing their potential for C sequestration (Xiao et al., 2021; Guimond et al., 2020).

Furthermore, soil CO₂ efflux consists of autotrophic respiration and heterotrophic respiration (Kutsch et al., 2010; Kuzyakov, 2006). Studying soil respiration and the characteristics of its components can be helpful in gaining insight into ecosystem C cycling processes (Kelting et al., 1998). Root exclusion is an indirect way to measure autotrophic respiration. The principle of this method is to calculate autotrophic respiration by measuring the difference between total soil respiration and nonroot respiration (Hanson et al., 2000). This method was used to investigate the contribution of autotrophic respiration to soil respiration in different ecosystems due to its simplicity, easy operation, and low destructiveness. However, we know little about the effects of bioturbation on soil respiration components in coastal BCEs.

Additionally, wetlands are generally sources of CH₄ to the atmosphere. Coastal wetland soils are rich in organic matter and anaerobic, making them suitable for CH₄ efflux despite of the sulfate-rich and saline environments (Kayranli et al., 2010; Figueiredo-Barros et al., 2009). These CH₄ effluxes are released into the atmosphere, offsetting approximately 10 % of the C buried in these coastal BCEs (Al-Haj and Fulweiler, 2020). The CH₄ efflux from wetlands can be altered by soil physicochemical factors (e.g., salinity, temperature, and nutrient concentration) as well as climatic conditions (e.g., rainfall) and tidal amplitude (Al-Haj and Fulweiler, 2020). Therefore, crab disturbances may also affect soil biogeochemistry and CH₄ efflux (Yuan et al., 2021). Although the effect of biological disturbance is essential, few studies has been done to investigate it.

The net impact of crab disturbances on GHG efflux in vegetated marshes is more ambiguous than that in their nonvegetated counterparts due to the limited amount of datasets. While a negative relationship between infauna and belowground biomass suggests that dense roots and networks limit the available space for burrowing activity (Gribsholt and Kristensen, 2002), the cumulative impact of burrows and vegetation on GHG from marshes has not often been quantified due to the lack of data on the abundance of burrows. Available results indeed propose that burrows still enhance CO₂ exported out of the sediment (Fanjul et al., 2015). However, it is predicted that the role of burrows might be minor in vegetated marshes due to the limited space for borrowing activity mentioned previously.

The present study was designed to assess the impact of burrowing behavior of the dominant fiddler crab, *Minuca pugnax*, on soil CO₂ and CH₄ efflux within the saltmarshes of Cape Cod, Massachusetts, USA. We hypothesized that (a) vegetation would affect the size of the burrows and therefore diminish their impact on soil CO₂ and CH₄ efflux; (b) crab burrows positively impacted the soil CO₂ efflux from the saltmarsh; (c) crab burrows would decreased soil CH₄ efflux.

2. Materials and methods

2.1. Study site

The study was conducted in the summer of 2018 within a natural saltmarsh located at the outlet of the Herring River in Wellfleet, Cape Cod, Massachusetts, USA (41°55'53.5"N 70°03'58.8"W; elevation ~1.4 m) (Fig. 1a). The study site was cut off from the Herring River estuary by the Chequessett Neck dike, constructed in 1908, and remained one of the few natural marshes along the estuary. The water table typically ranged from –20 cm to 10 cm inundation (Wang et al., 2019). This marsh was dominated by the native marsh grass *Spartina alterniflora* (over 90 % coverage), with an average shoot height of 30 cm, and hosted various burrowing crabs (Fig. 1b). Every sampling site was at the same elevation. More plant community information about this study site can be found by Heberlein (2016). The dominant species were two fiddler crabs: *Minuca pugnax* and *Leptuca pugilator* (Ocypodidae) and the purple marsh crab *Sesarma reticulatum* (Sesarmidae) (Bertness, 1985). We chose to conduct the study in areas dominated by *M. pugnax* and colonized, to a lesser extent, by *S. reticulatum*. Burrows of both species could be easily distinguished; *M. pugnax* burrows had a circular opening and housed one individual per burrow (Bertness and Miller, 1984). *S. reticulatum* burrow openings were larger, not circular, generally showed an inclination at the sediment surface, and the burrow was shallower with multiple surface openings (Bertness et al., 2014). *M. pugnax* burrows were chosen as the focus of this study due to their high density throughout the marsh and appropriate burrow opening size to fit within the available measuring equipment.

A three-way full factorial design was developed to assess the effect of *M. pugnax* burrow density (high and low), *S. alterniflora* presence/absence and high vs low organic matter content on soil CO₂ and CH₄ efflux. Two contiguous areas in the high marsh area with different organic matter contents (high and low) were selected by loss on ignition (Heiri et al., 2001). The top 10 cm of the sediment was dried at 65 °C and incinerated at 550 °C. Loss on ignition (LOI) was calculated based on dry-weight and ash-weight. After identifying high and low organic matter areas, a nonvegetated mudflat and a nearby saltmarsh vegetated patch were selected. The densities of *M. pugnax*, and *S. reticulatum* burrows were assessed across each area and patch along two 15 m long transects parallel to the bank of the bay. Five quadrats (24.5 × 24.5 cm) were randomly selected along each transect and all burrows were counted.

2.2. Burrow dimensions and morphology

To estimate the dimensions (surface area and volume) of *M. pugnax* burrows, casts were obtained using a polyester resin (Polymer Planet, marine-grade DCPD type resin, and methyl ethyl ketone peroxide, MEKP, hardener). The casts were carefully retrieved by hand or using a gardening shovel, returned to the lab, rinsed, and measured. Burrow depth was calculated as the orthogonal distance from the burrow opening to the deepest part of the cast using a measuring tape. The cast surface area was determined from the length of the tape with a known width wrapped around the entire cast, ensuring that the tape did not overlap itself. The original burrow wall surface area was hence assessed by calculating the area of the tape-based on its length and diameter (Bartolini et al., 2011). The burrow cast volume was estimated from the height of water displacement when placing the cast within a water-filled cylinder of known diameter.

2.3. Flux rate measurements

We measured soil CO₂ and CH₄ efflux along two transects of 7.6 m within each patch of each area during the low tide. PVC collars (10.2 cm in diameter) were placed along these transects. The collar places were selected in the vegetated saltmarsh patch to ensure no living

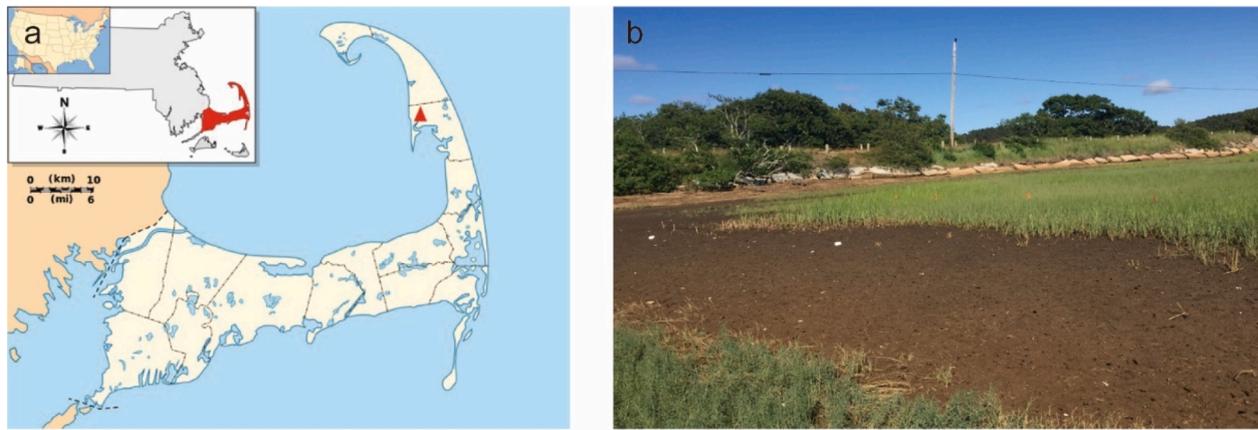


Fig. 1. Location of the saltmarsh sampling site (indicated with the red triangle) within the outlet of the Herring River in Wellfleet, Cape Cod, Massachusetts, US ($41^{\circ}55'53.5''\text{N } 70^{\circ}03'58.8''\text{W}$) (a). In this area, most of the saltmarshes have been restricted by dikes hampering seawater flow inland (b) (Portnoy and Giblin 1997). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

S. alterniflora shoots inside. All the collars were slightly pushed 4–5 cm into the sediment to ensure that the collar and chamber were completely sealed off when measuring gas flux. Based on our previous investigation, we found that the range of crab burrow in this study site was approximately 20 to 400 burrows per square meter. Therefore, in this experiment, the crab burrows density was set to three different crab burrow densities, which were 0, 122, and 367 burrows per square meter, respectively. Active burrows were identified based on the presence of an individual inside and well-maintained burrow openings. The burrow opening surface area was assessed for each flux measurement that included burrows. The maximum and minimum burrow opening diameters of the elliptical opening were measured before flux measurements. A minimum distance of 30 cm was kept from the *S. reticulatum* burrows to prevent measurement interference. Replicate measurements along each transect were displaced more than a meter from each other, and treatments did not cross one another. Two replicates for each crab burrow density category were measured every week for four consecutive weeks within each area (high vs low organic matter) for each patch (vegetated and nonvegetated) along each transect (within each patch). For each crab burrow category, a total of 12 replicates were measured, with 144 measurements taken in total.

Measurements were made by connecting a 6.3 cm tall \times 11.4 cm diameter non-transparent chamber, with a fan installed inside to keep air circulating to an LGR ultraportable CO_2 , CH_4 , and H_2O Analyzer (LGR Corp, CA, USA). The chamber was placed on top of the PVC collars. Pressure equilibration occurred through plastic tubing connected to the chamber and in contact with the atmosphere for an average of 5 min before starting a new measurement. Soil CO_2 flux measurements lasted 5 min per treatment (with approximately 10 s sampling intervals), based on observed periods for linear rates of gas concentration change and to avoid excessive chamber warming (Martin and Moseman-Valtierra, 2015; Brannon et al., 2016). Measurements were made an hour after the collars were placed (Pülmanns et al., 2014), and plants were cut off at their base to avoid CO_2 release due to the setup.

2.4. CO_2 and CH_4 efflux calculation

The following formula was used to determine soil CO_2 and CH_4 efflux:

$$F = (dc/dt) \times (1/V_0) \times (P/P_0) \times (T_0/T) \times (V/S) \quad (1)$$

where F is the flux rate, dc/dt is the slope of the greenhouse gas concentration vs time, V_0 is the molar volume under standard conditions (e. g., 22.4 L mol^{-1}), P is the air pressure at our study site, P_0 is the normal air pressure, T is the air temperature during each measurement, T_0 is the

standard temperature, V is the headspace volume of the chamber. S is the soil surface area within the collar. Only flux data with coefficients of determination (R^2) of the linear regression higher than 0.95 were used. In this study, soil CO_2 efflux rates from the saltmarsh area were defined as soil respiration, as there were no living shoots in each collar. In contrast, in the adjacent unvegetated mudflat area, it was defined as heterotrophic respiration. Autotrophic respiration was calculated by soil respiration minus heterotrophic respiration (Ren et al., 2017). Due to the limitation of the methods in determining the soil respiration components, the autotrophic microbial respiration was ignored in this study. The greenhouse gas emission calculation was conducted in Matlab (MATLAB and Statistics Toolbox Release 2016a, The MathWorks, Inc., Natick, MA, United States), using a code developed by Eckhardt and Kutzbach (2016).

2.5. Statistical analysis

One-way analysis of variance (ANOVA) and post hoc analysis with Tukey's test were carried out to test the differences between treatments at different respiration fractions. A generalized linear model fitting the data using Kendall's tau rank correlation coefficient was used to test the correlation between dependent variables (e.g., CO_2 flux, CH_4 flux) and independent variables (e.g., burrow surface area, volume). To determine the relation between GHG and environmental factors, we fitted a generalized linear mixed model (GLMM) (Bates et al., 2015) with a negative binomial error structure, including the sampling site as a random factor. The level of organic matter, vegetation type, and crab burrow density were fixed factors. As repeated measurements were conducted on selected sites at different times, the sampling data were nested as a random factor within sampling sites. The *glmm.hp* package (Lai et al., 2022) was used to elucidate the relative importance of each fixed effect factor. Moreover, the constructed model was diagnosed with the R packages 'PERFORMANCE' (Ludecke et al., 2021) to verify the normality of residuals and the collinearity of variables. All statistical analyses were performed at a significance level of 0.05. All analyses were performed with R v.4.0.4 software.

3. Results

3.1. Biotic and abiotic parameters

LOI for patches in the high organic matter zone were $23.5 \pm 1.8 \%$ (mean \pm SE) and $15.8 \pm 1.1 \%$ for nonvegetated and saltmarsh vegetated patches, respectively, while in the low organic zone, they were $4.8 \pm 0.2 \%$ and $3.8 \pm 0.1 \%$, respectively. Patches of saltmarsh were

characterized by 217 ± 26 shoots m^{-2} (max = 416), and there was no difference between low and high soil organic matter sites. The densities of *S. reticulatum* and *M. pugnax* burrows were $13 \pm 3 m^{-2}$ (max = 67) and $41 \pm 4 m^{-2}$ (max = 117), respectively.

There was a significant difference in soil organic matter content between the areas with rich and poor organic matter ($p < 0.01$) and significantly higher organic matter content was discovered in non-vegetated than saltmarsh patches ($p < 0.01$). On the other hand, there was no significant difference in saltmarsh shoot density between high and low organic matter areas ($p > 0.5$). No difference was noticed in the densities of purple marsh crab (*S. reticulatum*) burrows between rich and low organic matter content areas ($p > 0.5$) and vegetated and non-vegetated patches ($p > 0.5$). The density of *M. pugnax* burrows was not significantly different between areas characterized by high and low organic matter content ($p > 0.5$) or between vegetated and non-vegetated patches ($p > 0.5$). Thus, we could apply a full-factorial design to analyze the impact of different burrow densities across such environmental factors. At all sites, the abundance of burrows of *M. pugnax* was two to five times than that of *S. reticulatum*, showing to be the dominant species in these marshes.

3.2. Burrow morphology and its impact on greenhouse gas efflux

Burrow surface area and volumes were measured in this study (Fig. S1). The results showed that the structure of *M. pugnax* burrows significantly varied between vegetated and non-vegetated areas with an area of approximately $4.2 \pm 0.8 cm^2$ and a volume of approximately $24.1 \pm 11.3 cm^3$ in non-vegetated patches compared to an area of approximately $4.3 \pm 1.3 cm^2$ and a volume of $7.2 \pm 5.3 cm^3$ for vegetated patches (Fig. 2). There was no significant difference in crab burrow surface area between the nearby un-vegetated mudflat and saltmarsh ($p > 0.05$; Fig. 2a). The crab burrow volume within saltmarshes was significantly smaller than that within mudflats ($p < 0.05$), but the organic matter content had no effects on the crab burrow volume under the same vegetation type ($p > 0.05$) (Fig. 2b).

Soil CO_2 fluxes increased linearly with burrow volume ($p < 0.05$; Fig. S2c) but not with burrow surface area (Fig. S2a). There were no relationships between soil CH_4 fluxes and either the burrow volume (Fig. S2d) or burrow surface area (Fig. S2b).

3.3. Soil CO_2 efflux and its components

The average soil CO_2 efflux rates in the saltmarsh and nearby

unvegetated mudflats were $537.26 \pm 35.77 mmol m^{-2} d^{-1}$ and $301.47 \pm 42.23 mmol m^{-2} d^{-1}$, respectively (Fig. 3). To explore the factors regulating the soil CO_2 efflux rates, GLMM was applied to test the effects of soil organic matter, vegetation type, and crab burrow density. Soil CO_2 efflux rates significantly increased with organic matter ($p < 0.001$), vegetation type ($p < 0.001$), and burrow density ($p < 0.001$; Table 1; Fig. S3). The sampling time did not significantly affect the soil CO_2 efflux rates when the fixed effects and random effects were combined (Table 1). In the final model, soil organic matter had the highest individual contribution to the variation, followed by vegetation type and crab burrow density (Fig. S4a). Model diagnosis indicated that residuals for GLMM were mostly distributed normally (Fig. S5a), and collinearity did not exist among the variables (Fig. S5b).

The heterotrophic respiration rates were significantly higher in the patches with higher organic matter ($p < 0.05$; Fig. 4b), and crab burrows significantly enhanced heterotrophic respiration ($p < 0.05$; Fig. 4b). Soil autotrophic respiration increased with soil organic matter ($p < 0.05$) but not with crab density (Fig. 4a). However, the percentage of autotrophic respiration in soil respiration decreased with increasing soil organic matter and crab burrow density ($p < 0.05$ for both; Fig. S6).

3.4. Soil CH_4 efflux

The average CH_4 efflux from soils in the presence and absence of saltmarsh vegetation were $136.67 \pm 17.47 \mu mol m^{-2} d^{-1}$ and $12.58 \pm 1.82 \mu mol m^{-2} d^{-1}$, respectively (Fig. 5). The soil CH_4 efflux rates significantly increased with the increasing burrow density ($p < 0.05$), organic matter level ($p < 0.001$), and vegetation type ($p < 0.001$; Table 1; Fig. S7). In the soil CH_4 efflux model, vegetation type contributed the highest variation, followed by organic matter and the density of crab burrows (Fig. S4b). In addition, the soil CH_4 efflux diagnosis showed that residuals for GLMM were distributed normally (Fig. S5c), and no collinearity was found in the variables (Fig. S5d).

4. Discussion

4.1. Crab burrow morphology

Burrowing is important to crabs as it provides various functions (Nordhaus et al., 2009). One of the main reasons that crabs burrow into the sediment is to regulate their temperature (Eshky et al., 1995). When the surrounding temperature is too high, crabs start to dig into a cooler area. This study found that the crab burrows in saltmarsh vegetation

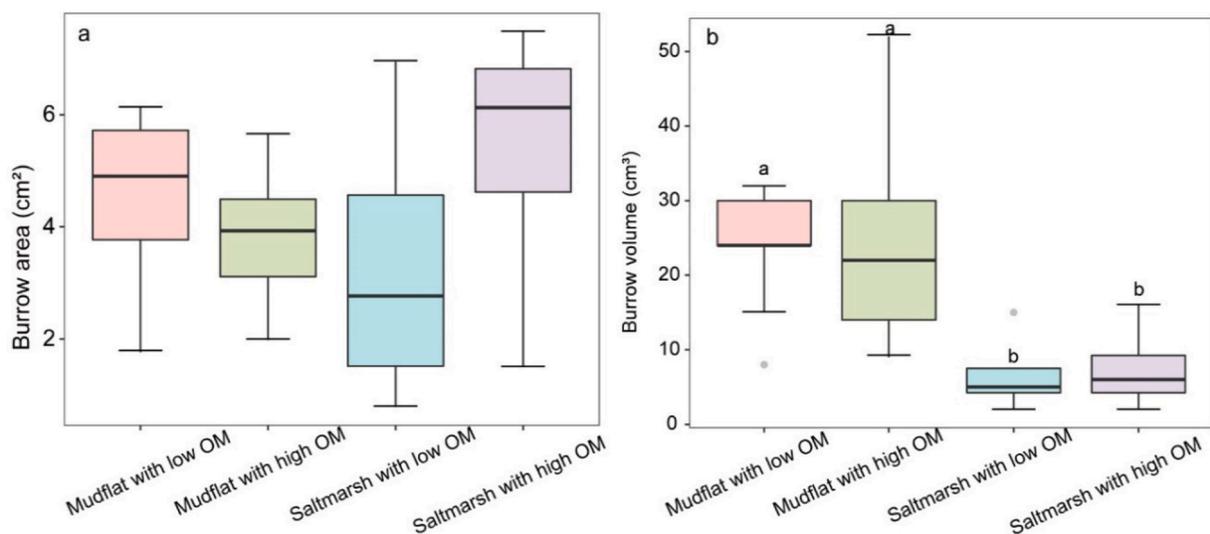


Fig. 2. Effects of different vegetation types and organic matter concentrations on the area (a) and volume of crab burrows (b). Lowercase letters indicate statistical significance ($p < 0.05$) among each treatment. OM, organic matter.

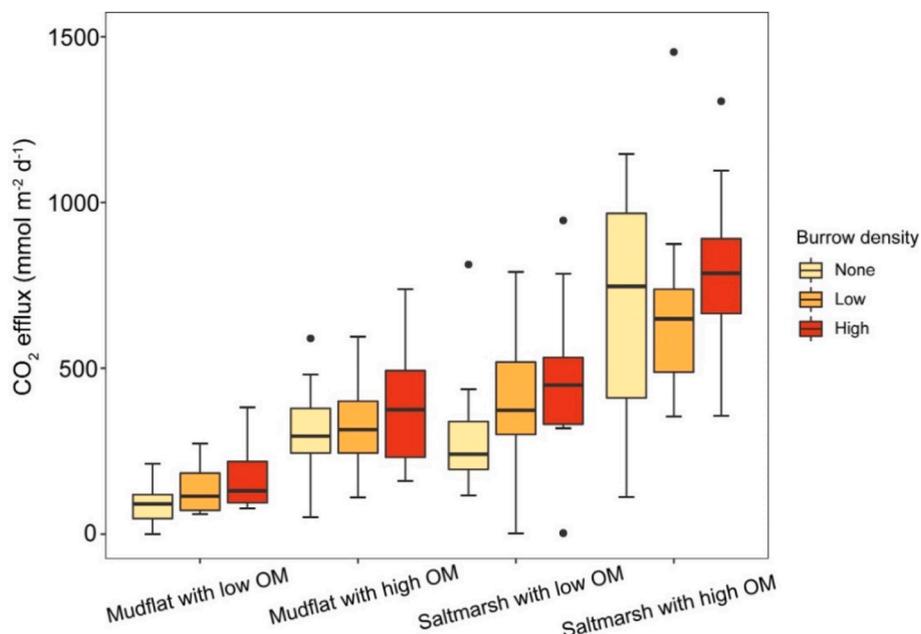


Fig. 3. Effects of different vegetation types, organic matter concentrations and crab burrow densities on CO₂ efflux. OM, organic matter.

Table 1

Statistical summary of generalized linear mixed model analysis on the effects of fixed factors such as burrow density, organic matter (OM) level, vegetation type, and random factors such as sampling dates on soil gases (CO₂ and CH₄) efflux rates.

Predictors	Soil CO ₂ efflux		Soil CH ₄ efflux	
	Estimates	p	Estimates	p
(Intercept)	23.297	0.787	-27.28	0.408
Burrow density	62.96	<0.001	11.92	<0.05
OM level	373.19	<0.001	51.03	<0.001
Vegetation type	235.79	<0.001	123.83	<0.001
Random Effects				
σ ²	1.626		9765	
τ _{00time}	14184.16		1926	
Marginal R ² /Conditional R ²	0.37/0.50		0.27/0.43	

were shallower and shorter. Shading by saltmarsh vegetation reduces the temperature rise caused by sun exposure; thus, crabs dig relatively shallow burrows to create a suitable environment (Chen et al., 2007). The other reason is that crabs can easily excavate the burrows in mudflats without the interference of densely tangled roots (Wang et al., 2015), while in saltmarsh vegetation, plant roots hinder the movement of crabs (Ringold, 1979). Similar conclusions can be found in other studies (Otani et al., 2010; Wang et al., 2015). Hence, it is difficult for crabs to cut dense roots and burrow into the sediment. Mudflats have larger crab burrows than saltmarsh, but no difference was found in the area of crab burrows (Fig. 2). This may suggest that the density of the crab burrows in saltmarsh is higher than that in mudflat, which can be interpreted by a broader range of food sources and a more suitable environment for the crabs (Li et al., 2015).

In addition, the crab burrows may act as primary water flow conduits in wetlands, increasing the C exchange between the soil-water interfaces (Xiao et al., 2021). The concentrations of dissolved inorganic

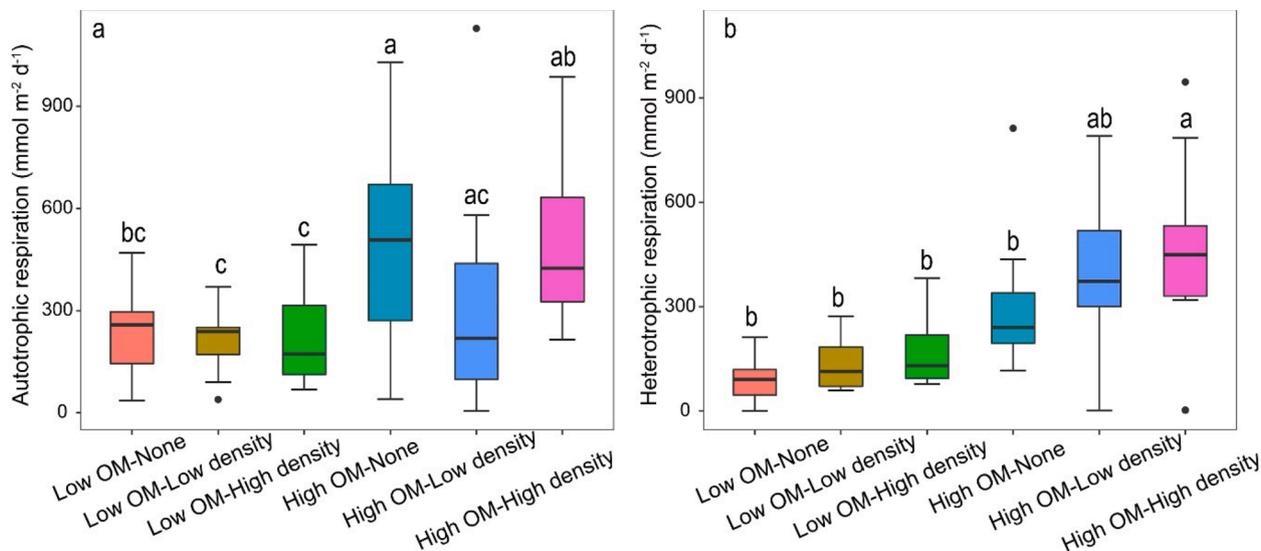


Fig. 4. Effects of different organic matter concentrations and crab burrow densities on autotrophic respiration (a) and heterotrophic respiration (b). Small letters indicate statistical significance ($p < 0.05$) among each treatment. OM, organic matter.

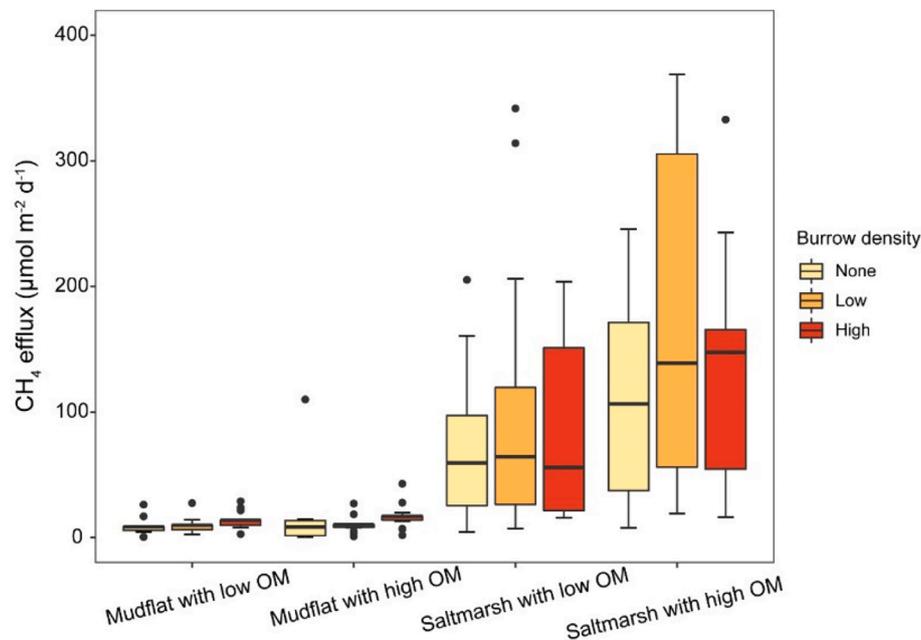


Fig. 5. Effects of different vegetation types, organic matter concentrations and crab burrow densities on CH₄ efflux. OM, organic matter.

and organic C in crab burrow porewater were higher than those in the surrounding soil, indicating the diffusion of C flux in the low-permeability marsh soil (Xiao et al., 2021). Regarding the shape of the crab burrow, we found that the shape of the crab burrow was mainly j-shaped, consistent with other reports (Otani et al., 2010), which was related to the living habits of the crab burrow, and the j-shaped burrows helped the crabs avoid tidal flushing.

4.2. Soil CO₂ efflux and its components

Our results highlighted that the presence and density of burrows increased the overall soil CO₂ efflux of this New England saltmarsh (Fig. 3), consistent with our second hypothesis. Similar results have been observed in some coastal wetlands; for example, Sasaki et al. (2014) reported that soil CO₂ efflux was more than tripled as a result of the crab biological disturbance in an estuary, and Tomotsune et al. (2020) found that the existence of burrows in mangroves increased the efflux of CO₂ by 1.1–1.6 times. This can be explained by the processes of diffusion-driven gas flux of saltmarsh sediments (Fenchel, 1996; Katz, 1980), as crab burrows increased the effective interface area, which could increase the oxidizing effect and promote oxidation of organic C (Tomotsune et al., 2020; Grow et al., 2022). The lower soil CO₂ efflux recorded for the low organic matter might be due to the limited amount of organic matter constraining the oxidation (Raich and Potter, 1995; Alongi et al., 2000). The much higher soil CO₂ efflux in the saltmarsh than that in the nearby mudflat patches (Fig. 3) might be explained by the soil autotrophic respiration (Raich and Potter, 1995; Wigand et al., 2009) in the vegetated saltmarsh, which contributed approximately 43.9 % of the soil CO₂ fluxes.

Soil respiration components changed after the existence of crabs. This suggested that the increasing burrowing activities in crabs may help to promote the survival of various microorganisms (aerobic or anaerobic bacteria) (Chen and Gu, 2017; Laverock et al., 2014), which, in turn, led to the changes in soil heterotrophic respiration that can ultimately affect biogeochemistry processes in coastal BCEs (An et al., 2021; Chen et al., 2021; Bang and Lee, 2019). Some variability among the patches with no burrows also implies the need for more extensive studies to fully document the role of burrowing on CO₂ release in coastal BCEs.

4.3. Soil CH₄ efflux

Under anaerobic conditions, CH₄ is released by methanogens in the final step of the anaerobic decomposition of soil C compounds (Young and Crawford, 2004). As observed in this experiment, soil CH₄ efflux was positively associated with high organic matter and burrows density. The crab's consumption of the plant litter could increase the soil organic C accumulation and then promote the growth of methanogens, leading to increased CH₄ production and efflux (Kammann et al., 2009). However, Li et al. (2015) reported that crabs reduced CH₄ effluxes. This was because the crabs would necessitate drastic movements, which reduced the availability of substrates for soil CH₄ production (Frei et al., 2007). The existence of saltmarsh vegetation also increased soil CH₄ fluxes in this experiment (Fig. 5), suggesting that the plant community in saltmarshes greatly regulated soil CH₄ efflux. Similar results have been obtained in some studies (Bhattacharyya et al., 2013; Datta et al., 2009). A previous study found that root exudates of plants served as a substrate for methanogens to promote soil CH₄ efflux (Wang et al., 2016; Robroek et al., 2015), and further study is needed to understand the specific mechanism of plant roles in saltmarsh CH₄ efflux.

5. Implications

Many studies have estimated the CO₂ and CH₄ efflux from coastal BCEs (Rosentreter et al., 2018; Kristensen et al., 2008b). For example, Leopold et al. (2015) reported that the rate of CO₂ efflux ranged from 0.71 to 2.41 mmol C m⁻² h⁻¹ in semiarid mangroves in New Caledonia, and He et al. (2019) estimated the efflux of CH₄ (1.29 mg CH₄ m⁻² h⁻¹) in a mangrove in China. However, most studies have not considered the impact of crab burrows on GHG efflux (Ouyang et al., 2017; Pongparrn et al., 2009). This study highlighted the importance of the presence or absence of crab burrows in estimating GHG efflux from BCEs, and C sequestration in coastal BCEs might be reduced by the existence of crab burrows. Moreover, BCEs vegetation type also affected the morphology and distribution of crab burrows. In this study, vegetated saltmarshes greatly reduced the volume of crab borrows compared with mudflats. Li et al. (2015) reported that crab burrow density in the mangrove vegetation area was higher than that of mudflats. Even in the same community, the vegetation canopy cover may also increase burrow density (Chen et al., 2007). Therefore, to estimate the C budget accurately, it is

necessary to consider the crab burrows in coastal BCEs.

6. Conclusion

Fiddler crabs play a critical role in biogeochemical processes in coastal BCEs (Kristensen and Alongi, 2006; Huhta, 2007). This study found that the crab burrow volume within saltmarshes was significantly smaller than that within mudflats. The soil CO₂ and CH₄ efflux rates significantly increased with the increasing burrows density, organic matter level, and the existence of vegetation type. The disturbance of crabs increased soil CO₂ and CH₄ efflux by 81.5 % and 60.0 % in the mudflats, respectively. Meanwhile, crab activity increased soil CO₂ and CH₄ efflux in the saltmarsh vegetation by 12.7 % and 51.7 %, respectively. Ultimately, our results highlighted the importance of considering burrowing activity when evaluating the potential C sequestration capacity of coastal BCEs.

CRedit authorship contribution statement

Laura E. Agosto: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Guoming Qin:** Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Benoit Thibodeau:** Formal analysis, Writing – review & editing. **Jianwu Tang:** Conceptualization, Data curation, Funding acquisition, Writing – review & editing. **Jingfan Zhang:** Writing – review & editing. **Jinge Zhou:** Writing – review & editing. **Jingtao Wu:** Writing – review & editing. **Lulu Zhang:** Writing – review & editing. **Poonam Thapa:** Writing – review & editing. **Faming Wang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – review & editing. **Stefano Cannicci:** Conceptualization, Formal analysis, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109538>.

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