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Effects of fiddler crab (*Minuca rapax)* feeding activity on mangrove sediment geochemistry

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ABSTRACT

Fiddler crabs are important ecosystem engineers in intertidal environments due to their intense sediment processing during feeding. Although their bioturbation activity has been widely studied, the specific effects of feeding behaviour on sediment geochemistry in mangrove systems remain poorly quantified. This study evaluated the effects of fiddler crab (*Minuca rapax*) feeding activity on sediment granulometry and chemical composition in a mangrove tidal flat at the Juréia-Itatins Ecological Station (southeastern Brazil). Sediment and feeding pellets were collected from 35 crab burrows and combined into composite samples for sedimentological and chemical analyses. Granulometry and organic matter content were compared between processed and surrounding sediments, while nutrient and mineral concentrations were analyzed using spectroscopic methods. Repeated-measures ANOVA and two-sample t-tests indicated that feeding activity did not significantly alter sediment granulometry or organic matter content. However, Ca (two-sample t-test) and Mg (Wilcoxon test) concentrations were significantly higher in feeding pellets, suggesting selective particle processing and mineral enrichment associated with feeding. These results indicate that *M. rapax* feeding activity contributes to localized geochemical modification of mangrove sediments without substantially altering sediment structure. Overall, our findings reinforce the ecological role of fiddler crabs as ecosystem engineers influencing nutrient redistribution and sediment geochemistry in mangrove environments.

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Highlights

- Calcium and magnesium concentrations increase due to *Minuca rapax* feeding activity.
- Feeding activity by *M. rapax* does not significantly alter sediment granulometry.
- Organic matter content remains unchanged despite feeding activity.
- Crab-induced geochemical processes influence nutrient cycling in mangroves.
- The role of fiddler crabs as ecosystem engineers reinforces their ecological importance in mangroves.

Introduction

In tropical and subtropical estuarine systems, mangroves are recognized for their high productivity, efficient nutrient recycling, and decomposition dynamics (Twilley et al. 1986; Sherman et al. 2003; Kristensen et al. 2008). The organic matter in these ecosystems can either be retained or transported by tides and currents to neighboring coastal environments, playing a crucial role in their ecological functioning (Lee 1995; Jennerjahn and Ittekkot 2002). The hydrodynamic and topographic features of mangroves create distinct areas (Icely and Jones 1978; Ewel et al. 1998), that exhibit variations in nutrient and organic matter availability

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and granulometric composition. These conditions give rise to distinct microhabitats and a rich diversity of species (Schwamborn et al. 2002; Sun et al. 2022; Vasconcelos Ramos et al. 2023), underscoring the importance of preserving these unique habitats (Sandilyan and Kathiresan 2012; Cannicci et al. 2021).

Crabs (Decapoda, Brachyura) are among the most abundant inhabitants of mangrove ecosystems (Crane 1975; Ellison 2008; Alongi 2009), with particular prominence given to the families Sesarmidae Dana, 1851 and Ocypodidae Rafinesque, 1815, which frequently dominate local assemblages and play key roles in sediment processes (Ashton and Macintosh 2024). Within the family Ocypodidae, fiddler crabs (subfamily Gelasiminae Miers, 1886) play a crucial role in mangrove sediment bioturbation (Kristensen 2008), influencing the chemical and physical properties of the substrate. Their burrowing and burrow-maintenance activities modify sediment by increasing its porosity and water content (Botto and Iribarne 2000), facilitating the transport and redistribution of nutrients and organic matter (Karlson et al. 2007; Natálio et al. 2017), and altering its redox potential (Nielsen et al. 2003). Through these processes, fiddler crabs stimulate nutrient exchange between water and sediment, organic matter remineralization, and microbial activity, thereby contributing to mangrove productivity (Mouton and Felder 1996; Botto and Iribarne 2000; Kristensen 2008; Sarker et al. 2021; Booth et al. 2023).

Although several studies on fiddler crab feeding behavior have been conducted in salt marsh environments, mangrove sediments differ in organic matter composition, sediment structure, and tidal hydrodynamics, which may influence sediment processing (Jennerjahn and Ittekkot 2002; Kristensen et al. 2008; Vasconcelos Ramos et al. 2023). Fiddler crabs and other deposit feeders consume sediment particles enriched with organic matter, including microphytobenthos, detrital material, and microbial biomass, modifying their granulometry (Sayão-Aguiar et al. 2012; Arbi et al. 2018; Medina-Contreras et al. 2020; Noghabi et al. 2022) and influencing processes such as primary production (Holdredge et al. 2010) and organic matter dynamics (Reinsel 2004)**.** The selective ingestion of these organic matter-rich fractions can influence the distribution and availability of organic matter in mangrove sediments. By altering the spatial distribution of organic matter and nutrients, they regulate the availability of essential elements to plants and other organisms (Kristensen 2008; Penha-Lopes et al. 2009; Holdredge et al. 2010; Citadin et al. 2016), highlighting the important role these animals play in the functioning of mangrove ecosystems. Beyond their ecological functions, the crabs' unique morphological adaptations (particularly their specialized mouthpart setae) allow fiddler crabs to selectively ingest smaller organic and inorganic particles (Miller 1961; Icely and Jones 1978; Maitland 1990; Colpo and Negreiros-Fransozo 2011), while discarding larger particles as feeding pellets near their burrows (Crane 1975; Maitland 1990; Di Virgilio and Ribeiro 2013). This feeding behavior results in localized sediment processing, which may influence the distribution of nutrients and mineral elements in mangrove sediments.

Bioturbation carried out by fiddler crabs such as *Minuca rapax* Smith, 1870 (Brachyura, Ocypodidae) is a key ecological process that influences soil geomorphology, stability, and overall functionality (Meysman et al. 2006). Additionally, it is essential for sustaining biodiversity and ensuring ecosystem functionality (Coleman and Williams 2002). Due to its wide distribution in the Western Atlantic (from Florida, USA, to Santa Catarina, Brazil) (Pinheiro and Boos 2016), ease of capture, and high abundance, *M. rapax* is a promising species for comparative studies between preserved and impacted areas (Capparelli et al. 2019). The species is common in sandy and exposed environments, with several burrows distributed at random. Density estimates previously conducted at the study site reported an average of 3.4 individuals·m^{-2} for *M. rapax*, with adult males comprising the majority (1.3 individuals·m^{-2}) (Carvalho et al. 2018).

Bioturbation and feeding activity of fiddler crabs are well documented (Gribsholt et al. 2003; Capparelli et al. 2022), although the specific effects of sediment processing during feeding on mangrove sediment geochemistry remain insufficiently quantified. This study investigates how feeding activity by *M. rapax* influences the properties of mangrove sediment by examining its impacts on granulometry, organic matter content, and nutrient composition. We hypothesized that sediment processing during feeding would modify the sediment's geochemical composition without significantly altering its granulometric structure. By testing this hypothesis, we aim to clarify the extent to which feeding activity contributes to localized geochemical modification of mangrove sediments. In doing so, we also contribute to a deeper understanding of the role of fiddler crabs as ecosystem engineers in nutrient redistribution and organic matter dynamics in mangrove ecosystems.

Material and methods

Study area

This study was conducted at the Juréia-Itatins Ecological Station (JIES) (24°25′57.5″ S – 47°05′56.1″ W), located on the southern coast of São Paulo, Brazil, and managed by the Forestry Foundation (FF) under the jurisdiction of the State Government (Figure 1). JIES is part of a vast network of protected areas and is recognized as a UNESCO World Heritage Site. The area is part of an estuarine system comprising several well-preserved rivers, characterized by semidiurnal tides ranging from 0.1–1.5 m (Por et al. 1984). Due to its exceptional state of preservation, JIES is classified as a pristine area and is frequently used for comparative studies on environmental quality (Duarte et al. 2016; Duarte et al. 2017). The selected mangrove flat is dominated by sandy sediments and supports abundant populations of fiddler crabs, particularly *M. rapax*, the dominant ocypodid species in this sector of the estuary (Figure 1).

Sampling design

Field sampling was conducted to compare the granulometry, organic matter content, and nutrient composition of non-bioturbated sediments and sediments processed by feeding activity (feeding pellets) produced by *M. rapax*. Sampling took place on a large tidal flat (~600 m^2) located about 120 m from the waterline, in an area with elevated topography, exposed sandy soil, and sparse shrub vegetation. This sector of the tidal flat is regularly exposed at low tide, and fiddler crabs exhibit intense surface activity. A summary of the sampling design and pooling strategy is presented in Table I.

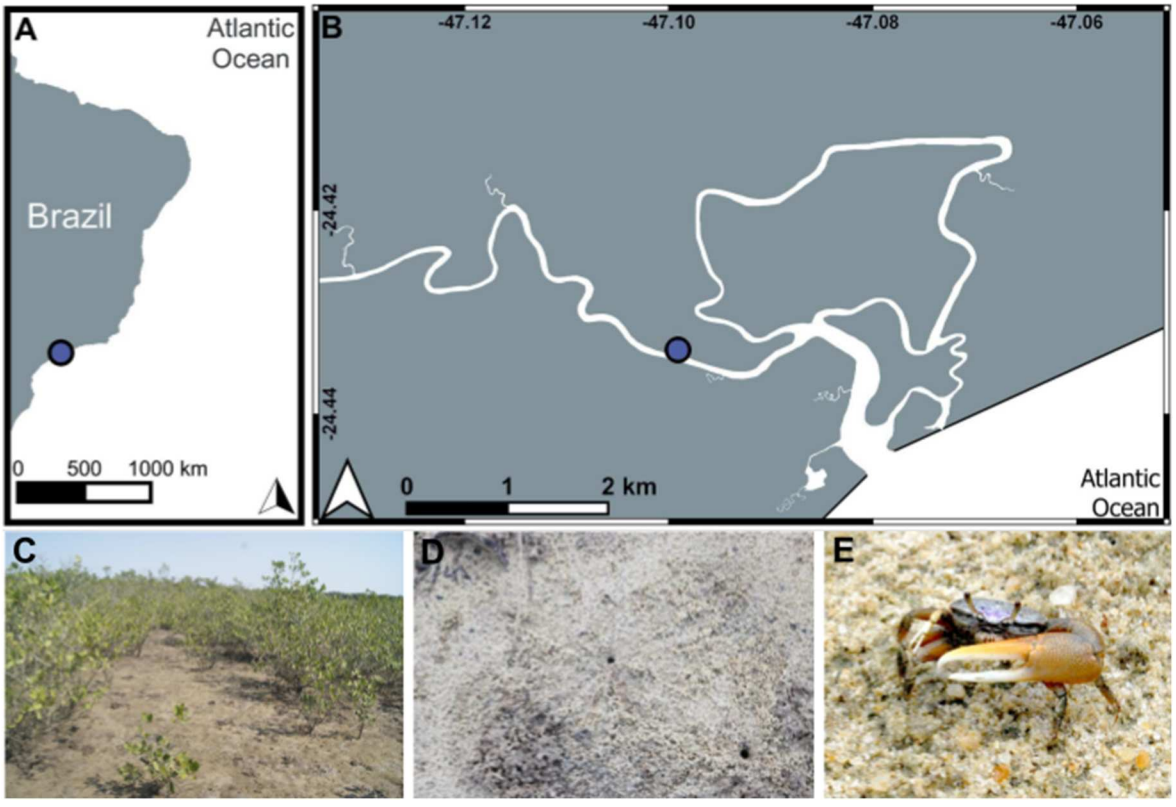

Figure 1. A, General view of the South America and southeast Brazilian coast; B, geographic position of the study area; C, mangrove area where samples were collected at the Juréia-Itatins Ecologic Station (JIES); D, frontal view of *Minuca rapax* Smith, 1870 (Brachyura, Ocypodidae) in the sediment; E, frontal view of adult male of *M. rapax* in the mangrove. [Photo credits: map of the studied area: A, B, Marcio João (CRUSTA – UNESP IB/CLP); C, D, Klaus Kriegler (CRUSTA – UNESP, IB/CLP); E, Luis Ernesto Bezerra – Universidade Federal do Ceará].

Table I. Summary of sediment samples collected to evaluate the feeding activity of Minuca rapax.

Sample type	Description	Collection method	Sampling unit	Pooling strategy	Final number of composite samples
Non-bioturbated sediment	Surface sediment not processed by crab feeding activity	Collected during low tide within a 15 cm diameter circular device placed around active burrow openings; sediment sampled to a maximum depth of 3 cm	Sediment surrounding each of the 35 selected burrows	Samples were pooled due to the limited amount obtained	9
Bioturbated sediment (feeding pellets)	Pellets produced during crab feeding activity	Collected during low tide around active burrow openings, using an oral aspirator; feces and excavation pellets excluded	Feeding pellets produced around each of the 35 selected burrows	Samples were pooled due to the limited amount obtained	9

Sediment collection

Sediment sampling was carried out in September-October 2018, during the regional dry season and spring tides, which provide extended exposure of intertidal sediments and facilitate the observation of feeding activity and collection of pellets. Sediment samples were collected over some days during daytime low tides, when fiddler crab feeding activity is most evident and feeding pellets are freshly produced.

To assess the effects of *M. rapax* feeding activity on sediment properties, 35 burrows were selected based on the presence of feeding pellets near their openings. Only burrows with visible biogenic activity that were sufficiently distant from neighboring burrows were selected, avoiding the collection or mixing of pellets from other individuals. This ensured that the collected pellets belonged exclusively to the focal animal. To standardize the number of samples collected from each burrow, a circular device (15 cm in diameter and 3 cm high) was positioned around the burrow openings. Then, using a spatula, we collected sediment inside this device, with a maximum depth of 3 cm (approximately 0.53 L of sediment). Because of the limited amount of sediment obtained, samples were pooled to form nine composite samples for each condition (non-bioturbated sediment and feeding pellets) (Wentworth 1922; Colpo and Negreiros-Fransozo 2011). Pooling was necessary to obtain sufficient material for the sedimentological and chemical analyses conducted here.

Although bioturbation in fiddler crabs may involve several processes (*e.g.* burrow excavation, sediment displacement, and burrow maintenance), the present study specifically focused on sediment processed during feeding activity. Therefore, the term 'bioturbated sediment' used in this study refers exclusively to sediment processed during feeding and deposited as feeding pellets. This operational definition allowed a comparison between non-bioturbated and bioturbated sediment (feeding pellets).

Feeding pellets

Feeding pellets were collected during low tide using an oral aspirator, while feces and excavation pellets were excluded from the samples, following the protocol outlined by Sayão-Aguiar et al. (2012), as our focus was to evaluate whether the feeding activity of *M. rapax* could alter organic matter, nutrient concentrations, and sediment granulometry. Fiddler crabs leave their burrows approximately four hours before low tide (Ribeiro et al. 2003), and feed for 2–3 h before sealing them, with a mean (±SE) duration of 3 h and 19.1 ± 12.1 min, and 50% of individuals exhibiting feeding times between 44.2 min and 1 h 42.2 min (Di Virgilio and Ribeiro 2013). Thus, the feeding pellets collected here were at most three hours old, minimizing potential alteration by tidal leaching, rainfall, or microbial degradation. This precaution ensured that the chemical composition of the feeding pellets closely reflected sediment conditions immediately after feeding.

Within each marked area (15 cm), composite samples of non-bioturbated sediment were collected to a maximum depth of 3 cm. Later, the burrow occupants ($n = 35$ adult males) were extracted using a spatula, identified and sexed according to Bezerra (2012) and Masunari et al. (2020), and measured for carapace width (CW), with a precision caliper (0.05 mm). Only males were included in the analyses to minimize variability related to sex-specific behavioral differences in feeding activity (Valiela et al. 1974; Mokhlesi et al. 2011). Both non-bioturbated sediment and feeding pellets were stored in refractory containers and dried in a ventilated oven at 60 °C for 72 h.

The organic matter content was quantified by wet oxidation with sulfochromic solution followed by colorimetric analysis (expressed in g·kg^{-1}). Macronutrient analysis included available phosphorus (P, mg·dm^{-3}), potassium (K), calcium (Ca), and magnesium (Mg, mmolc·dm^{-3}), all extracted using an ion-exchange resin and quantified by spectroscopy. The sum of bases (SB, mmolc·dm^{-3}) represents the sum of exchangeable cations (K^+, Ca^{2+}, Mg^{2+}). All analyses in this block were based on Raij et al. (2001).

Granulometry was analyzed using sieving and differential weighing for sand, silt, and clay fractions, together with the pipette method to separate silt from clay (Gee and Bauder 1986). Seven granulometric fractions were identified: 2–1 mm (very coarse sand, VCS), 1–0.5 mm (coarse sand, CS), 0.5–0.25 mm (medium sand, MS), 0.25–0.15 mm (fine sand, FS), 0.15–0.05 mm (very fine sand, VFS), 0.05–0.002 mm (silt, SIL), and < 0.002 mm (clay, CLA). VCS and CS were not found in the sediment samples.

Statistical treatment and data analysis

Statistical analyses were performed using R 4.5.1 (2025), following the statistical indications of Sokal and Rohlf (2012). Normality of nutrient and organic matter data was assessed using the Shapiro–Wilk test, and homogeneity of variances was assessed using the Bartlett test. Depending on the data distribution, parametric or non-parametric tests were applied: a t-test was used for parametric data (P, K, Ca, organic matter, and SB: sum of bases K^+, Ca^{2+}, Mg^{2+}), using the mean as the measure of central tendency; and a Wilcoxon test was used for non-parametric data (Mg), based on median contrasts. When the homogeneity of variances was not satisfied, Welch's t-test was applied. These tests assessed whether substance concentrations differed between non-bioturbated sediment and feeding pellets (Sokal and Rohlf 2012).

Extractive potential (EP%) was used as an index to estimate the proportion of organic matter removed from sediment during fiddler crabs' feeding. This index represents the difference between the organic matter content of sediment collected inside burrows (SOM) and that of feeding pellets deposited outside the burrows (POM). The calculation of EP% was adapted from Sayão-Aguiar et al. (2012) as follows:

$$EP\% = [(SOM - POM)/SOM] \cdot 100$$

Higher EP% values indicate greater removal of organic matter from sediment during fiddler crab processing.

The granulometry, organic matter content, and nutrient data were analyzed to compare statistical differences between non-bioturbated and feeding-processed sediments. For granulometric analysis, comparisons were made both (i) within the same granulometric fraction between sediment types (non-bioturbated and feeding pellets), and (ii) among granulometric fractions within each sediment category. Because granulometric fractions from the two sediment categories were derived from the same sampling units, comparisons between sediment types were conducted using a one-way repeated measures ANOVA, followed by Tukey's *post hoc* test. The significance level was set at 5%.

Additionally, the relative proportions of granulometric fractions (MS, FS, VFS, SIL, and CLA) between sediment types were compared using a two-tailed z-test. This test was used to evaluate whether the proportional representation of each granulometric fraction differed significantly between non-bioturbated sediments (SED) and feeding pellets (PEL), assuming a standard normal distribution.

To characterize sediment texture, the SysGran software was employed to calculate the mean grain size (φ), which was then converted to millimeters, along with classification, skewness, and kurtosis (see De Camargo 2006). Moreover, non-bioturbated sediment and feeding pellets were classified based on Pejrup's hydrodynamic criteria (Pejrup 1988) and Shepard's textural classification (Shepard 1954).

To complement the univariate analyses, a multivariate approach was used to assess overall differences in geochemical composition among non-bioturbated and bioturbated sediments (feeding pellets). Organic matter, P, K, Ca, Mg, and SB were standardized (z-scores) prior to analysis to eliminate scaling differences between variables.

Multivariate variation patterns were explored using Principal Component Analysis (PCA), based on the correlation matrix of the standardized variables. The contribution of each variable to the principal components was assessed using loading scores.

Differences in overall geochemical composition among non-bioturbated and bioturbated sediments (feeding pellets) were tested using a Permutational Multivariate Analysis of Variance (PERMANOVA), based on Euclidean distances and 999 permutations. To verify whether the significant PERMANOVA

results could be attributed to differences in intragroup dispersion rather than differences in centroid location, the homogeneity of multivariate dispersions was assessed using PERMDISP. All multivariate analyses were performed in R using the *FactoMineR*, *factoextra*, and *vegan* packages.

Results

The collected fiddler crabs had a carapace width (CW) ranging from 7.6–19.0 mm (mean ± standard deviation: 12.3 ± 3.7 mm). All individuals analyzed corresponded to adult males actively feeding on the sediment surface during the sampling period.

Sediment granulometry

For the granulometric fractions (Figure 2), no significant differences were observed between non-bioturbated sediment and feeding pellets (repeated measures ANOVA: $F = 0.38$; $df = 32$; $p = 0.82$). This indicates that sediment processing during feeding did not significantly modify the granulometric structure of the substrate.

However, significant differences were found within each sediment category (non-bioturbated and feeding pellets), with a clear predominance of very fine sand (VFS: 62.3%) and fine sand (FS: 36.8%) in both sediment types (repeated measures ANOVA: $F = 267.60$; $df = 32$; $p < 0.01$) (Figure 2).

The two-tailed z-test comparing granulometric fractions between non-bioturbated and feeding-processed sediments revealed no significant differences in the proportion of each granulometric fraction between the two categories.

In the granulometric analysis using SysGran, the mean particle size (φ) ranged from 3.21 in the non-bioturbated sediment to 3.24 in the feeding pellets, both classified as very fine sand.

Both non-bioturbated sediment and feeding pellets were categorized as poorly sorted, exhibiting strong positive skewness (0.352 for non-bioturbated sediment and 0.369 for feeding pellets). The kurtosis values were highly leptokurtic in both categories, ranging from 1.85–2.02, respectively.

The Shepard diagram classified both sediment categories (non-bioturbated and feeding pellets) as sandy silt (Figure 3A), while the Pejrup diagram indicated very high hydrodynamics (classification IV) (Figure 3B).

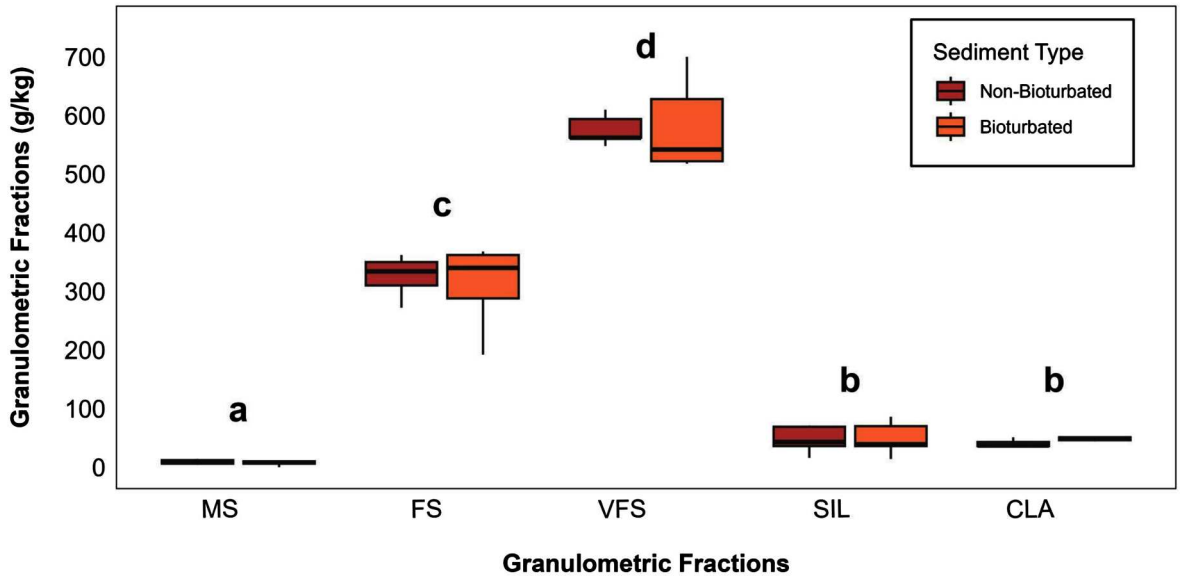

Figure 2. Quantitative evaluation and significance of granulometry in five fractions (medium sand, fine sand, very fine sand, silt, clay) associated with non-bioturbated and bioturbated sediment samples (feeding pellets). Where: the box plot shows the median (horizontal line), interquartile range (IQR, represented by the box), whiskers (1.5 times the IQR), and black dots indicate outliers. No significant differences ($p < 0.05$) were found when comparing each granulometric fraction between non-bioturbated and bioturbated sediments. However, significant differences were detected among granulometric fractions within each category, as indicated by different letters (Tukey's HSD, $p < 0.05$).

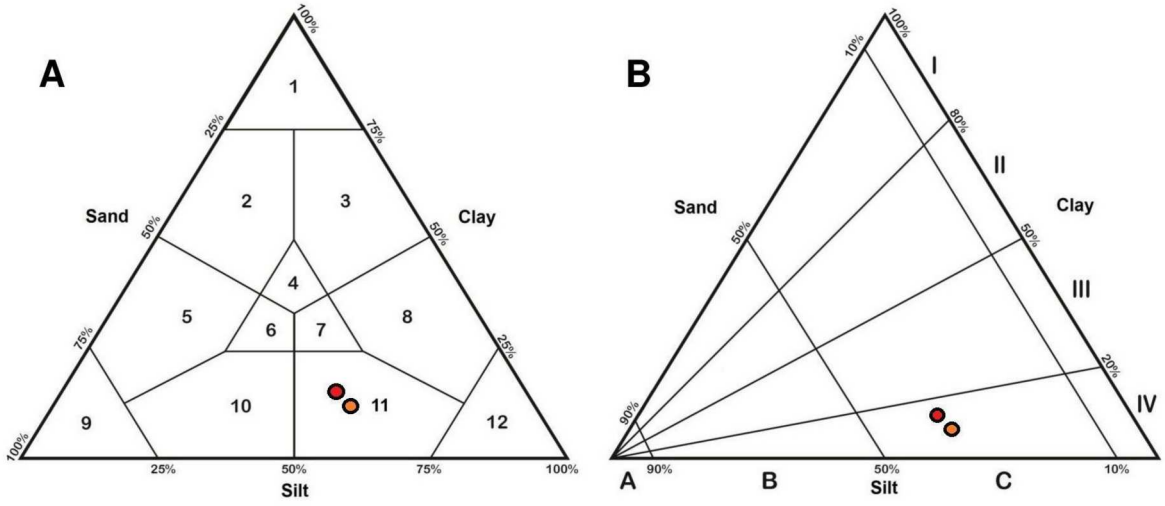

Figure 3. Classification of non-bioturbated (in orange) and bioturbated sediment samples (feeding pellets, in red) according to granulometry (A: Shepard diagram) and hydrodynamics (B: Pejrup diagram). In A: 1, clay or claystone; 2, sandy clay; 3, silty clay; 4, silty sandy clay; 5, clayey sand; 6, silty clayey sand; 7, clayey sandy silt; 8, clayey silt; 9, sand or sandstone; 10, silty sand; 11, sandy silt; and 12, silty or siltstone. In B: I, low hydrodynamics; II, moderate hydrodynamics; III, high hydrodynamics; IV, very high hydrodynamics.

These sedimentological results confirm that both sediment categories belong to the same textural and hydrodynamic regime, reinforcing the absence of major structural changes in sediment composition after feeding activity.

Organic matter

The organic matter concentration in the non-bioturbated sediment (mean ± standard deviation: 17.1 ± 2.5 g·kg^{-1}) did not differ significantly from that in the feeding pellets (15.1 ± 3.0 g·kg^{-1}) (two-sample t-test: t = −1.58; df = 16; $p = 0.13$) (Figure 4). Although the mean OM content was slightly lower in the feeding pellets, the difference was not statistically significant.

The EP% of organic matter by *M. rapax* was estimated at 11.7%.

Mineral composition

Regarding nutrients, P and K showed no significant differences between non-bioturbated sediment and feeding pellets (Table II; Figure 5). In contrast, Ca, Mg, and the SB exhibited statistically significant differences. Ca was significantly higher in the feeding pellets (25.5 ± 5.3 mmolc·dm^{-3}) compared to non-bioturbated sediment (12.7 ± 4.0 mmolc·dm^{-3}) (two-sample t-test: t = 5.03; df = 8.76; $p < 0.01$). A similar pattern was observed for Mg (71.0 ± 4.7 mmolc·dm^{-3} in the feeding pellets versus 39.1 ± 15.4 mmolc·dm^{-3} in the non-bioturbated sediment) (Wilcoxon test: W = 54; $p < 0.01$) and for the SB (K^+, Ca^{2+}, Mg^{2+}) (100.2 ± 10.5 mmolc·dm^{-3} in the feeding pellets versus 55.2 ± 19.1 mmolc·dm^{-3} in the non-bioturbated sediment) (two-sample t-test: t = 5.86; df = 12.73; $p < 0.01$) (Table II; Figure 5).

These results indicate that sediment processed during feeding activity contained higher concentrations of divalent cations, particularly Ca^{2+} and Mg^{2+}, resulting in a substantial increase in the total pool of exchangeable bases in the processed sediment.

Multivariate analysis of sediment geochemistry

PCA revealed a clear separation between non-bioturbated sediments and feeding pellets, indicating differences in overall geochemical composition associated with fiddler crab feeding activity (Figure 6). The first two principal components explained 84.7% of the total variance, with PC1 accounting for 57.6% and PC2

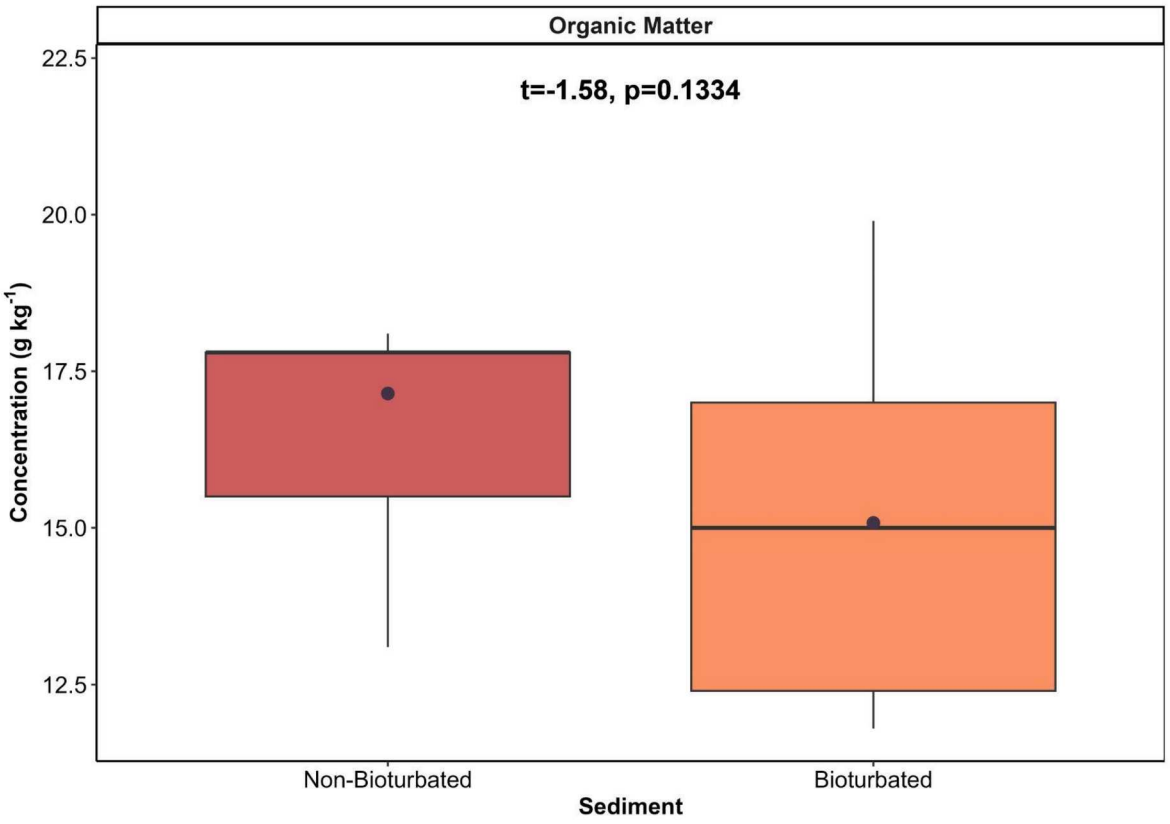

Figure 4. Organic matter concentration in non-bioturbated and bioturbated sediment samples (feeding pellets). Where: the box plot shows the median (horizontal line), interquartile range (IQR, represented by the box), and whiskers (1.5 times the IQR); t, t-test; p, probability value.

for 27.1%. The PCA ordination showed limited overlap between sediment categories and distinct group centroids, suggesting a consistent shift in sediment geochemistry following sediment processing by *M. rapax*.

The PERMANOVA confirmed significant differences in overall geochemical composition between non-bioturbated sediments and feeding pellets (Pseudo-F = 7.45, $R^2 = 0.364$, $p = 0.001$). The test for homogeneity of multivariate dispersions was not significant (PERMDISP: F = 0.005, $p = 0.953$), indicating that the observed multivariate differences resulted from shifts in group centroids rather than unequal dispersion among samples.

Discussion

The feeding activity of *M. rapax* did not significantly alter sediment granulometric composition or organic matter content, but increased the concentrations of Ca, Mg, and SB in the bioturbated sediment (feeding

Table II. Nutrient concentrations, fertility, and acidity in non-bioturbated and bioturbated (feeding pellets) mangrove sediment samples associated with the burrows of the fiddler crab Minuca rapax. Means (or medians) of the same chemical variable followed by the same letter did not differ statistically according to the significance level established by the t-test or Wilcoxon test, respectively. Where: *P* = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, OM = organic matter, SB = sum of bases (K^+, Ca^{2+}, Mg^{2+}).

	Sediment (mean ± standard deviation)			
Chemical Variables	Non-Bioturbated Sediment	Bioturbated Sediment (Feeding Pellets)	t-test* / Wilcoxon**	*p*
P (mg·dm^{-3})	3.6 ± 0.9 a	3.3 ± 1.3 a	−0.56*	0.59
K (mmolc·dm^{-3})	3.4 ± 1.0 a	3.7 ± 0.8 a	0.73*	0.48
Ca (mmolc·dm^{-3})	12.7 ± 4.0 a	25.5 ± 5.3 b	5.33*	< 0.01
Mg (mmolc·dm^{-3})	39.1 ± 15.4 a	71.0 ± 4.7 b	54.00**	< 0.01
OM (g·kg^{-1})	17.1 ± 2.5 a	15.1 ± 3.0 a	−1.58*	0.13
SB (mmolc·dm^{-3})	55.2 ± 19.1 a	100.2 ± 10.5 b	5.23*	< 0.01

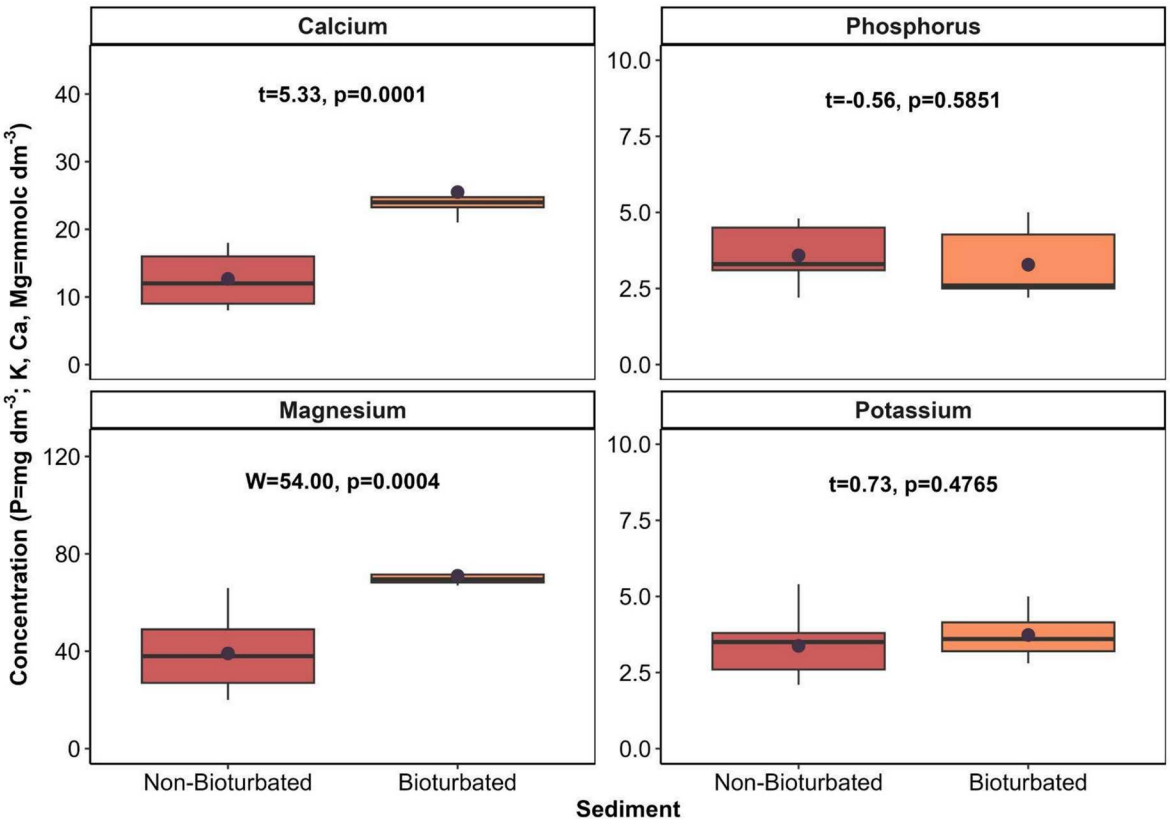

Figure 5. Nutrient concentration in non-bioturbated and bioturbated sediment samples (feeding pellets). Where: the box plot shows the median (horizontal line), interquartile range (IQR, represented by the box), and whiskers (1.5 times the IQR); t, t-test; W, Wilcoxon test; p, probability value.

pellets). These results indicate that sediment processing associated with feeding activity primarily influences sediment geochemistry rather than its physical structure. The organic matter EP% of this species was 11.7%, a relatively low value. Fiddler crabs and other deposit feeders often reduce the amount of organic matter they consume (Citadin et al. 2016). In this process, they selectively extract microphytobenthos, microbial communities, and particles with a high organic matter content (Maitland 1990; Penha-Lopes et al. 2009; Citadin et al. 2016). Thus, the feces of these animals generally contain lower concentrations of organic matter compared to the surrounding sediment. Although a similar trend was observed in the present study for the feeding pellets, the reduction was not statistically significant, possibly due to the low organic matter content and sandy conditions of the study area. Studies evaluating the organic matter content in bioturbated sediments resulting from the feeding activity of fiddler crabs are scarce (Wolfrath 1992; Colpo and Negreiros-Fransozo 2011); for example, Citadin et al. (2016) suggested that excavation pellets may contain higher organic content than feeding pellets.

Together, these results reinforce the idea that the ecological effects of fiddler crab feeding activity may be expressed more strongly through chemical modification of sediments than through physical restructuring of the sediment.

Sediment granulometry

Fiddler crabs can modify their environment through bioturbation and feeding, thereby influencing grain size distribution (Jennerjahn and Ittekkot 2002; Sayão-Aguiar et al. 2012; Qin et al. 2024), nutrient concentrations (Kristensen 2008; Sun et al. 2022), organic matter content (Natálio et al. 2017; Neely 2023), and even microplastic dispersion (Capparelli et al. 2022). However, in the present study, the feeding activity and deposition of feeding pellets by *M. rapax* did not significantly alter sediment grain size. Botto and Iribarne (2000) demonstrated that fiddler crabs can alter sediment grain size through burrow construction; but, in our

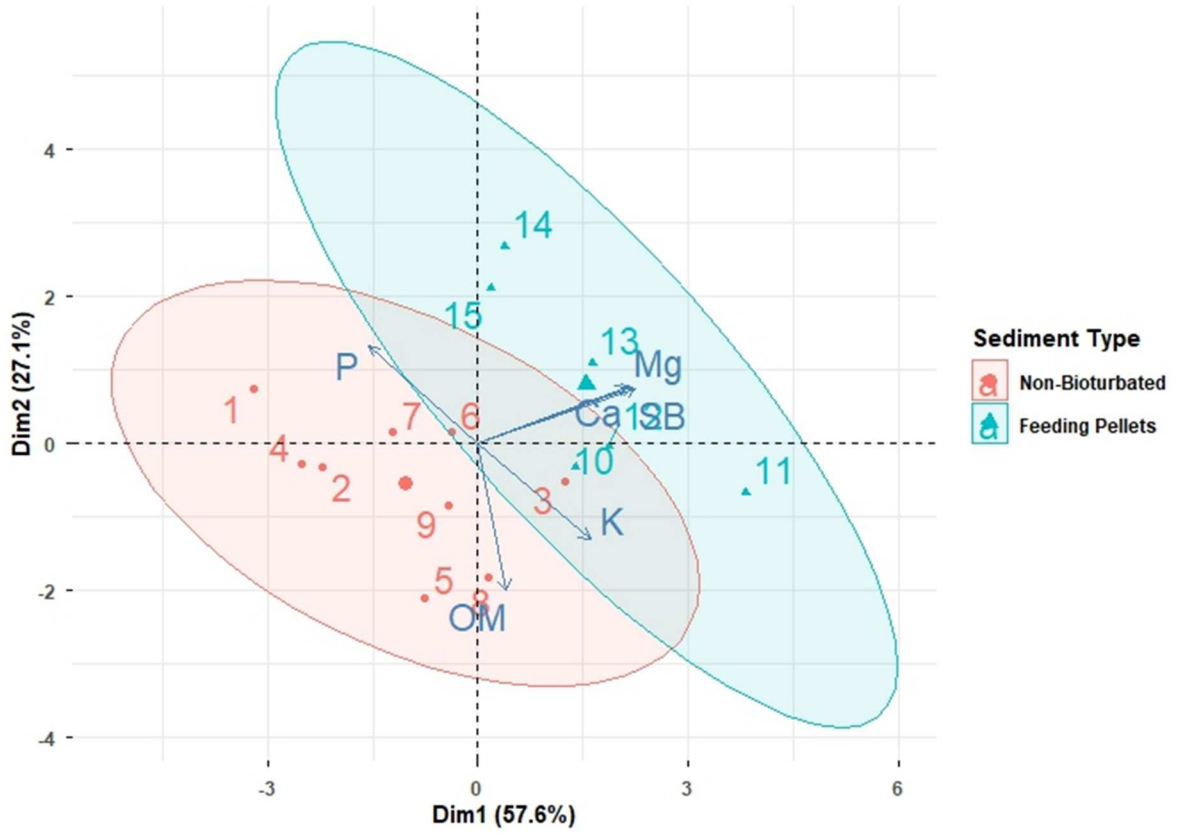

Figure 6. Principal Component Analysis (PCA) using a biplot function. A total of six variables were used, from two sediment types (non-bioturbated and feeding pellets). Where: OM, organic matter; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; and SB, sum of bases (K^{+}, Ca^{2+}, Mg^{2+}).

case, differences occurred only among granulometric fractions within each sediment type (non-bioturbated and feeding pellets).

Other studies have observed that the feeding activity of *M. rapax* and other fiddler crabs modifies sediment composition (Colpo and Negreiros-Fransozo 2011). During feeding, these deposit feeders ingest smaller grains enriched with organic matter (Miller 1961; Ribeiro and Iribarne 2011; Di Virgilio and Ribeiro 2013), while discarding larger, indigestible particles as feeding pellets around their burrows (Crane 1975; Kristensen 2008).

The absence of significant differences in sediment granulometry here may be attributed to the predominance of fine-grained fractions (fine and very fine sand) in the study area, with coarser fractions (coarse or medium sand) being virtually absent. Although feeding pellets often contain a higher proportion of coarse particles, in this case even the largest fractions were classified as fine.

Analyses performed using Sysgran software indicated that both non-bioturbated and bioturbated sediments (feeding pellets) exhibit similar composition, being classified as sandy silt, a characteristic of areas with high hydrodynamic energy. These results align with those reported by Ribeiro et al. (2005), suggesting that variations in sediment grain size are not solely driven by bioturbation, but are also influenced by local hydrology.

Organic matter

The results may indicate selective feeding behavior toward particles with higher organic content (Valiela et al. 1974; Meziane et al. 2002), coupled with low EP%. Male crabs have higher energy demands due to their larger size and weight, and therefore spend more time foraging (Valiela et al. 1974; Mokhlesi et al. 2011; Tina et al. 2015). This increased feeding effort may enhance sediment turnover even when the net extraction of organic matter remains relatively low. Although females feed faster, this does not necessarily

imply differences in overall feeding efficiency or in their ability to alter sediment nutrient content (Valiela et al. 1974; Pinheiro and Boos 2016).

Here, only males were used due to behavioral differences in feeding between the sexes (Valiela et al. 1974; Mokhlesi et al. 2011). Nevertheless, the feeding activity of *M. rapax* contributed to the redistribution of nutrients in mangrove sediments, increasing Ca, Mg and the SB concentrations. Therefore, if females were included as well, the results would likely be similar. Future studies should compare feeding activity between sexes.

The low organic matter content of the study area may have limited the availability of organic-rich particles, prompting *M. rapax* to seek alternative food sources, reinforcing its dietary adaptability. Fiddler crabs obtain organic matter from alternative sources, such as macroalgae, detrital mangrove litter, and even conspecific carcasses (Kim 2010; Nallos and Macusi 2023), as confirmed for *M. rapax* by De Grande et al. (2021), who reported that this species preys on other organisms, such as *Leptuca uruguayensis* Nobili, 1901 (Brachyura, Ocypodidae). Here, fiddler crabs were not observed feeding on any food sources other than sediment-associated material.

Mineral composition

The higher concentrations of Ca, Mg, and the SB in feeding pellets suggest that feeding activity promotes the redistribution of exchangeable bases in surface sediments. These elements are crucial for exoskeleton calcification in crustaceans and ionic balance (Henry et al. 2012; Eagon and Zou 2023). However, fiddler crabs do not obtain these nutrients exclusively from food attached to sediment particles but also from other food sources (Kim 2010; De Grande et al. 2021; Nallos and Macusi 2023) and through their gills (Greenaway 1985; Wheatly 1996). Therefore, the amount of nutrients absorbed by the crabs may exceed their physiological needs, resulting in the release of excess ions into the surrounding sediment.

The increase in the concentration of these elements in the sediment and the deposition of feeding pellets may benefit other organisms, such as plants, phytoplankton, and benthic invertebrates. This enrichment can increase primary production in the intertidal zone, promote plant and tree growth (Fusi et al. 2022), and enhance microphytobenthos abundance – an important food for various invertebrates and a key contributor to mangrove primary production (Botto and Iribarne 2000; Reinsel 2004; Kristensen 2008; Sayão-Aguiar et al. 2012).

Moreover, by contributing to nutrient cycling and spatial heterogeneity in sediment composition (Cohen et al. 1999; Bouillon et al. 2002; Kristensen and Alongi 2006; Cannicci et al. 2008; Colpo and Negreiros-Fransozo 2011; Yan and Hou 2018), *M. rapax* can enhance meiofaunal and microbial diversity (DePatra and Levin 1989; Colpo and Negreiros-Fransozo 2011), given that a male fiddler crab can produce around 400 feeding pellets per day (Yamaguchi 2000). The role of fiddler crabs as mediators of sediment fertility, through alterations in sediment chemistry and microbial community composition, reinforces their ecological relevance as ecosystem engineers in mangrove ecosystems (Booth et al. 2019).

By increasing Ca and Mg in the sediment, fiddler crabs can influence the cation exchange capacity and nutrient availability for primary producers (Reinsel 2004; Sun et al. 2022). Comparable processes have been documented in other bioturbating species, where sediment reworking enhances microbial activity, oxygen penetration, and organic matter remineralization (Kristensen 2008). Thus, the activity of *M. rapax* may indirectly contribute to regulating carbon and nutrient fluxes between water and sediment, helping maintain the stability and productivity of mangrove ecosystems (Yang et al. 2025).

Such processes highlight the importance of bioturbating crabs in mediating the coupling between biological activity and sediment geochemistry in intertidal environments. The multivariate analyses further support this interpretation. Although univariate tests detected significant differences only for Ca, Mg, and SB, the PCA and PERMANOVA demonstrated that fiddler crab feeding activity produced a consistent shift in the overall geochemical composition of the sediment. This result indicates that the effects of sediment processing by *M. rapax* extend beyond isolated changes in individual variables and are reflected in the integrated geochemical profile of feeding pellets.

Synthesis

The present study demonstrated that the feeding activity of *M. rapax* can promote bioturbation of mangrove sediments and increase the concentrations of certain nutrients (Ca, Mg, and SB) without significantly altering

organic matter content or grain size. Although this species' organic matter EP% is relatively low (approximately 12%), this value aligns with the dietary diversity of *M. rapax*.

Sayão-Aguiar et al. (2012), however, reported a higher organic matter extraction for this species (37.5%), suggesting that this parameter varies with sediment availability, although it remains lower than the 88.1% potential recorded for *L. uruguayensis*. The authors attribute this difference to the lower number of spoon-tipped setae on the second maxilliped, indicating a more generalist feeding behavior in *M. rapax* compared with the specialized feeding of *L. uruguayensis*.

Future studies quantifying organic matter and nutrient content in alternative food sources could provide a more comprehensive understanding of the diet of *M. rapax* and its role in biogeochemical cycling in mangrove ecosystems. Such investigations would also help clarify which components are effectively assimilated from different food sources, offering valuable insights into the ecological role and functional plasticity of this species.

Study limitations

Some limitations of the present study should be acknowledged. Sampling was restricted to a relatively short time interval and therefore represents a temporal snapshot of sediment conditions within the study area. Seasonal variability may influence both crab activity and sediment properties in mangrove ecosystems. Additionally, the analyses were conducted exclusively on male individuals, who were the most frequently observed feeding on the sediment surface in the study area during the sampling period. Although male fiddler crabs typically exhibit higher surface activity, potential differences between the sexes cannot be ruled out and should be investigated in future studies.

Despite these limitations, our results provide new evidence that the feeding activity of *M. rapax* contributes to localized geochemical modification of mangrove sediments without substantially altering sediment texture.

Future investigations incorporating seasonal sampling and additional trophic analyses would further clarify the ecological implications of these processes.

Conclusions

The present study demonstrates that the feeding activity of *M. rapax* does not significantly modify sediment granulometry or organic matter content but promotes detectable changes in sediment geochemistry by increasing Ca, Mg, and the SB in feeding pellets. These findings indicate that the ecological influence of this species is expressed primarily through geochemical modification rather than through changes in the sediment's physical structure.

By redistributing nutrients during feeding and pellet deposition, *M. rapax* contributes to nutrient cycling and sediment heterogeneity in mangrove environments. This process may enhance nutrient availability for benthic microorganisms, primary producers, and other invertebrates, reinforcing the functional role of fiddler crabs as ecosystem engineers in intertidal systems.

Although the observed EP% of organic matter in this study was relatively low, the feeding behavior and dietary flexibility of *M. rapax* suggest that this species can exploit multiple food sources within mangrove habitats. Future studies integrating sediment chemistry, microbial dynamics, and alternative dietary sources will be essential to better understand the contribution of fiddler crabs to biogeochemical processes in coastal ecosystems.

Understanding these processes is essential for evaluating the role of bioturbating crustaceans in maintaining the productivity, nutrient dynamics, and ecological resilience of mangrove ecosystems. Such knowledge is particularly relevant for understanding the functioning and conservation of tropical mangrove systems.

Author contributions

CRediT: **Caio Augusto Paula:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing; **Nicholas Kriegler:** Conceptualization,

Investigation, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing; **Marcelo Antonio Amaro Pinheiro:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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No potential conflict of interest was reported by the author(s).

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Data availability statement

All authors would like to inform you that all the data used in the manuscript entitled 'Effects of fiddler crab (*Minuca rapax*) feeding activity on mangrove sediment geochemistry.' have been made available to ensure transparency and reproducibility of our study. The data are accessible through Mendeley Data (https://data.mendeley.com/datasets/5yj9gvvtf8/4), with the following identifier: doi:10.17632/5yj9gvvtf8.4.

We are available to provide any additional information or clarification that may be necessary.

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