A bioengineer in the city —the Darwinian fitness of fiddler crabs inhabiting plastic pollution hotspots☆

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ABSTRACT

Mangrove forests have been widely recognized as effective traps for plastic litter, which tends to accumulate in landward areas. In mangrove forests surrounding cities, plastic litter may increase up to two orders of magnitude. Therefore, crabs that process sediments for feeding and burrowing in landward areas are likely to be impacted by marine litter and other disturbances. As counterintuitive as it may seem, crabs are developing dense populations in urban mangroves from different countries, suggesting parallel adaptive processes related to the availability of anthropogenic food sources. To better understand this, we compared the loads of macroplastics within and between mangroves along an urban-rural-wild forest gradient in the Urabá Gulf, Colombian Caribbean. We then assessed if there is directional selection on crab phenotypes likely associated with human-provided food sources in urbanized forests. Finally, we evaluated the hypothesis that crabs in urban areas exhibit increased fecundity and survival - components of the Darwinian fitness - of female crabs in urban (versus wild) populations through three spawning seasons. Crabs in urban areas were larger (males), showed a healthier body condition (both sexes), and females had a larger reproductive lifespan than crabs in wild areas, strongly suggesting responses to the availability of predictable anthropogenic food subsidies in urban forests. Despite this, higher female fecundity was observed only during a spawning season. However, this short-lived increase in fecundity was offset by reduced survival among female crabs in urban forests, likely due to increased predation by birds, which appear to be emerging as dominant consumers in urban mangroves.

1. Introduction

The sequestration of plastic pollution in the benthic realm has been proposed as a mechanism explaining the low loads of plastics present in surface waters, with mangrove systems acting as the most effective sinks for these materials in coastal areas (Martin et al., 2020). Several inter-acting factors explain the sequestration of plastics in mangrove forests, including the architectural properties of aerial root systems, the dynamic of tidal cycles, the high sediment accretion rates and the influence of biological interactions on the buoyance of plastic materials (Ivar do Sul et al., 2014; Riascos et al., 2019; Martin et al., 2020). In addition, in mangrove forests surrounding urban areas plastic burial may be increased by two orders of magnitude, turning urban mangroves into one of the most polluted areas globally (Riascos et al., 2019). Hence, assessing the ecological and evolutionary implications of huge and

continuous additions of exogenous materials on marine species that have tailored evolutionary strategies for terrestrial life-styles in mangrove sediments is a compelling issue.

Fiddler crabs have long been recognized as key ecosystem engineers in mangrove forests (Kristensen, 2008). These crabs establish dense populations on intertidal flats, feeding on microalgae and bacteria. Through their crawling, foraging and burrowing activities fiddler crabs mobilize a significant amount of sediment, in the process changing abiotic setting (drainage, redox potential, nutrient availability and organic matter content) and shaping the structure of meiofaunal communities and primary producers (Ólafsson and Ndaro, 1997; Kristensen and Alongi, 2006; Penha-Lopes et al., 2009a). Therefore, it seems obvious that huge loads of exogenous anthropogenic materials would reduce the fitness of these highly specialized crabs. Macroplastic litter (*i. e.* plastic items ≥5 mm diameter) might be particularly problematic

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because it may hinder foraging and burrowing, as shown by the observed fragmentation of plastic materials through crab's feeding activities (So et al., 2023).

As counterintuitive as it may sound at first sight, some studies suggest that fiddler crabs seem to be thriving in human-disturbed systems. For example, Costa and Soares-Gomes (2015) observed that the biomass of *Minuca rapax* was higher in urban areas with strong anthropogenic eutrophication in Brazil. Similarly, fiddler crab biomass and species richness increased from non-urban to urban mangrove forests in Mozambique and Kenya (Cannicci et al., 2009). Indeed, Penha-Lopes et al. (2009b) hypothesized that the organic loading of urban wastewater may stimulate microbenthic primary production and sewage-derived detritus, leading to an increase in reproductive potential and quality of *Austruca annulipes* in Mozambique.

There is accumulating evidence showing that the strong selective pressures imposed by urbanization translate into consistent species phenotypic signatures, and these in turn, may have ecological and evolutionary implications (revised by Thompson et al., 2022). However, urban phenotypes with the potential to make ecological and evolutionary sense must: i) and display directional selection related to urban pressures, and ii) confer advantages in terms of *fitness* (i.e., a measure of genetic contribution to future generations) (Endler, 1986). As fitness itself is essentially impossible to measure, the best we can do is to measure fitness components. Reproductive success and survival have emerged as suitable measures of Darwinian fitness (Hendry, 2016; Koch and Narum, 2021). Hence, taking as a study model the fiddler crab *Minuca vocator* (Herbst, 1804) inhabiting a mosaic of urban and non-urban mangroves in the Urabá Gulf, our aims were threefold. Firstly, we wanted to quantify the differences in terms of amount of plastic materials between urban mangroves (local plus imported litter) and non-urban mangroves (imported litter). Secondly, we assessed if there is a directional selection on crab phenotypes likely related to increased food subsidies from humans in urban settings. Finally, we evaluated the hypothesis that urban phenotypes would increase the fecundity and survival of female crabs through age intervals in urban versus wild populations.

2. Materials and methods

2.1. Study area

The study was performed in mangrove forests located along the eastern border of the Urabá Gulf, an embayment being the southernmost region of the Caribbean Sea (Fig. 1). The oceanographic setting and dominant biomes of the Gulf are largely determined by the freshwater and sediment loads of the Atrato river –the second largest river in the Southern Caribbean (Beier et al., 2017). Being a tropical river deltaic system, the Gulf is mainly dominated by dense, almost monospecific (*Rhizophora mangle*) forests, considered one of the most productive mangrove forests in the world (Riascos and Blanco-Libreros, 2019). Although mangrove forests are mainly located in the southwestern border, those from the eastern border best exemplify a gradient of increasing human influence in the Gulf. Three mangrove areas were chosen for this study: Turbo, El Uno and Coquito Point (Fig. 1). Following the concept of anthropogenic biomes (*sensu* Ellis and Ramankutty, 2008), which uses human population density, land uses, and land cover types to classify terrestrial biomes, these three places have been previously studied and classified as Urban, Rural and Wild forests, respectively (Blanco-Libreros and Estrada-Urrea, 2015). Mangrove forests in Turbo city (Urban forest) remain in peri-urban areas and are submitted to several anthropogenic disturbances, including solid waste disposal, high deforestation rates, landfills for the construction of trails and houses and changed hydrologic regimes. The city is inhabited by 59, 761 people and lacks a public sewage system; hence four canals discharge sewage without treatment, one of them -Chocosito canal-directly impacting peri-urban mangrove forests. Mangroves in El
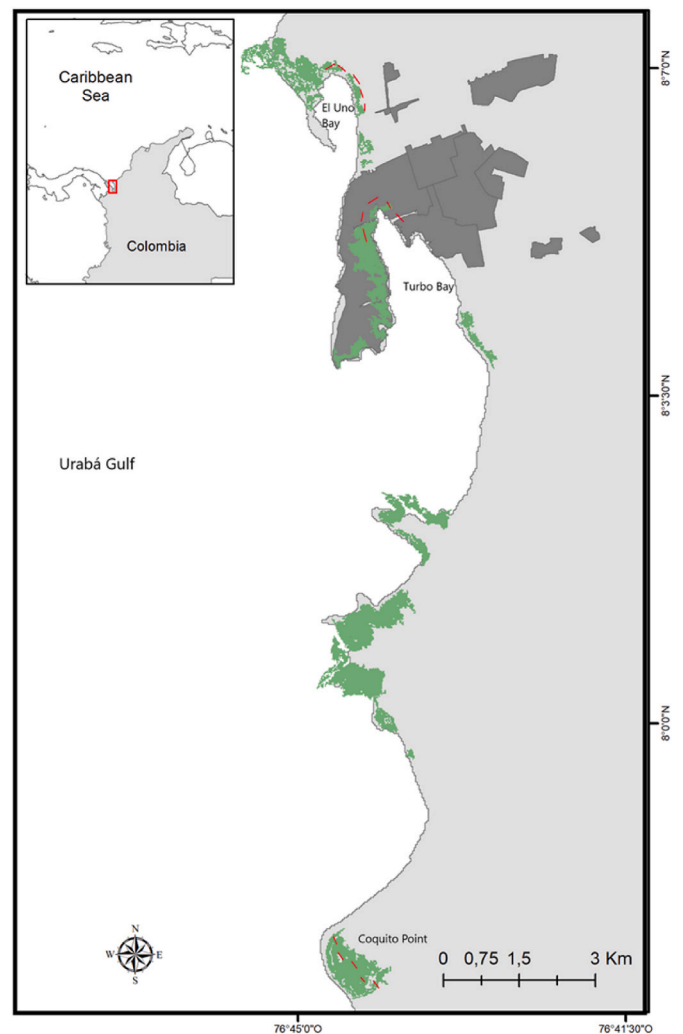

Fig. 1. Map of the study area and the three types of mangrove forests sampled in this work: El Uno bay (rural forest), Turbo bay (urban forest) and coquito Point (wild forest). The red lines in each forest show the transects used to sample the fiddler crabs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Uno bay (Rural forest) are affected by agricultural activities, land reclamation and moderate levels of urbanization; about 500 houses surround the bay and a small sewage canal discharge wastewater without treatment. In contrast, mangroves in Coquito Point (Wild forest) remain as a remote area, with little influence of urban expansion.

2.2. Sampling design and processing

2.2.1. Density of macroplastics in the sediment surface

The density (# items m^{-2}) of macroplastic litter (*i.e.* plastic items ≥5 mm diameter) in the surface sediment layer was surveyed at the beginning of this study (24–26 March 2022). For this, five transects perpendicular to the shoreline were placed in each type of mangrove forest. Transects were spaced 200 m apart, thus covering 1 km of mangrove belt approximately. In each transect, five circular plots (2 m diameter) were equidistantly located in the area between the transition zone with terrestrial vegetation and the low tide water mark. Macroplastics lying in the surface or semi buried within the circular plot were counted and collected to prevent double counting.

2.2.2. Fiddler crab sampling

Samplings were performed in two stagesThe first sampling was

performed in 24–26 March and aimed to assess directionality in crab phenotype through the three types of forests (Urban-Rural-Wild). The second stage aimed to assess crab fitness, for which additional samplings were taken in 23–24 April 23 and 24–25 May, only in the Urban and Wild forests, which represent the extremes of urban-related disturbances. These specific days and months were selected chosen based on the following reasons. Tropical fiddler crabs typically show continuous breeding seasons (Ahmed, 1976; Sastry, 1983). However, previous studies show that the relative number of ovigerous females of *M. vocator* increase at the beginning of the rainy season (Colpo and Negreiros-Fransozo, 2003; Koch et al., 2005). Rainfall in the study area increases between April and July and therefore an increase in reproductive activity is expected during the March–May period. On the other hand, hatching and larval release in this species is synchronous and timed to a semilunar cycle (four days before or after the maximum amplitude tide; Christy, 2011). Therefore, our samplings intended to register reproductive activity during three consecutive pulses of larval release.

Crab populations are usually distributed in a relatively narrow transition zone between mangrove and terrestrial vegetation, but they can occur in a wider area –extending to the low tide water mark– particularly in urban mangrove forests, where crabs occur in a highly heterogeneous landscape influenced by built structures. To account for this, the vegetal transition zone in each transect was taken as the starting point for crab samplings. A shovel was used to sample between 27 and 81 small $0,11\ m^{-2}$ plots haphazardly located from this starting point and seaward, in areas not covered by built structures. The number of plots varied to account for spatial variability in crab density and to obtain between 44 and 120 individuals (see Supplementary file 1). In each plot, crabs were excavated to 30–35 cm depth using metal shovels and the sediment removed was carefully examined, searching for fiddler crabs, and registering crab density (crabs m^{-2}). All the resulting crabs were placed in individual plastic jars with formalin and transferred to 90% ethanol for preservation after 24 h. In the laboratory, each crab was classified as female, ovigerous female, males or juveniles based on the sexual dimorphism in claws and telson (Crane, 1975). Thereafter, the size of crabs was measured (carapace width; mm) with vernier calipers.

2.3. Directional selection on crab phenotypes

Three phenotypic traits were measured at the beginning of the study (March 2022) to assess if they are being selected in any direction along the urban-wild gradient: i) the size range of female reproduction (indicative of the reproductive lifespan), estimated as the difference in body size between the largest and smallest ovigerous female in a given sample, ii) maximum body size of male and female crabs (quantified as the five largest individuals in each sample), and iii) body condition of males and females– a relative measure of the energetic or nutritional state of an individual animal under a given environment (*e.g.*, Riascos et al., 2008). Owing to the deficient performance of classical indices in accounting for the scaling relationship between mass and length (see Peig and Green, 2010), we used the scaled mass index of body condition (Peig and Green, 2009):

$$\widehat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where M_i is the body mass (g) and L_i the carapace width (cm) of individual i, b_{SMA} is the scaling exponent estimated by the standardized major axis regression of M on L for the study population, L_0 is an arbitrary value of L (in this case the arithmetic mean value of L for the study population); and $\widehat{M}_i$ is the predicted body mass for individual i when the linear body measure is standardized to L_0. The scaling exponent $bSMA$ was calculated from the linearized power equation:

$$\ln M = \ln a + b \times \ln L$$

Owing to strong sexual dimorphism in *M. vocator* and the expected effect on estimations of body condition, $bSMA$ was calculated for each sex.

Analyses of variance followed by Tukey's HSD tests for paired comparisons (or Kruskal-Wallis tests, followed by Dwass-Steel-Critchlow-Fligner tests when the assumptions of parametric tests were not meet) were used to assess differences in density (both sexes), maximum size (male and female) and body condition (male and female). These tests used the phenotypic traits as the dependent variable and forest type (urban, rural and wild) as an independent factor.

2.4. Female fecundity through age intervals

Male fiddler crabs are promiscuous, while females are highly selective in mate choice. Hence, the reproductive success depends on the number and fecundity of females that males can attract (Greenspan, 1980; Johnson, 2003). For this reason, we studied the fecundity of female crabs during three reproductive pulses (March, April, May) in the urban forest and the wild forest. To estimate fecundity (the number of eggs per female), ovigerous females were dissected under a stereomicroscope to remove pleopods. Thereafter they were placed in petri dishes filled with seawater and eggs were detached by gradually adding sodium hypochlorite. Bare pleopods were then discarded, and eggs were suspended by gently stirring in a beaker filled with 50 ml seawater. Three 1.5 ml aliquots were taken using a pipette, and eggs counted under a dissecting microscope. The resulting average value was then extrapolated for the whole suspension to estimate the number of eggs (Flores and Paula, 2002). These data were used to assess the variability in female fecundity through age intervals in Urban and Wild forests in each reproductive pulse. For this, the mean fecundity of females in monthly age intervals was fitted to a linear regression using ln-transformed age data. Significant differences in the regression slopes for urban and wild forests in each reproductive period were assessed using T-tests. Obtaining direct measurements of age was beyond the scope of this study. Therefore, age intervals were estimated considering the parameters K (the growth coefficient) and L_∞ (the theoretical length at which the growth of an organism is halted) of the von Bertalanffy Growth Function and the index of growth performance phi prime (ϕ') reported by Koch et al. (2005) for female *M. vocator* in northern Brazil. It is known that the parameters K and L_∞ are often site-specific. This is reflected in the fact that the maximum length registered in our study area was larger than the L_∞ reported from northern Brazil. However, several authors (Pauly, 1979; Munro and Pauly, 1983; Sparre and Venema, 1992) showed that ϕ' can be used as a species-specific estimation of growth performance, owing to the inverse relationship between the parameters K and L_∞:

$$\phi' = \log K + 2 \times \log L_\infty$$

Thus, the maximum length observed for female *M. vocator* among 3358 individuals measured was taken as a realistic estimation of L_∞ in the study area. Therefore, K was obtained from the above equation, maintaining ϕ'constant and L_∞ as the maximum length.

2.5. Female survival

Finally, length-frequency distributions of female crabs were used to analyze the changes in survival through ontogeny and relative abundance of female crabs producing eggs in the Urban and Wild forest during the reproductive pulses. For this, the abundance of female crabs in 1 mm-size ranges was converted to relative abundances (%), to account for differences in sample size.

3. Results

3.1. Macroplastic density

The density of macroplastic litter in surface sediments showed two distinctive features (Fig. 2a). First, the mean density of plastic litter observed in the urban forest was one order of magnitude higher (75.70 ± 1.28 items m^{-2}; mean ± SE) than that observed in rural (4.86 ± 1.57 items m^{-2}) and wild (5.00 ± 1.59 items m^{-2}) mangrove forests. Second, while the density of plastics decreased seaward in the urban forest, the opposite was observed in the rural and wild forest.

3.2. Directional selection on crab phenotypes

In total, 3358 crabs were collected in this study. Some behavioral differences were observed in *M. vocator* inhabiting urban areas. They occupied a much wider area, extending from the supra-littoral to the meso-littoral in the intertidal zone. Moreover, they inhabited more diverse microhabitats, compared with crabs in wild or rural mangroves, which are generally restricted to the supra-littoral zone. These mico-habitats included wastewater canals, permanently flooded areas below houses and trails, wooden logs and landfills (Supplementary file 2). All these microhabitats had macroplastic items, either buried or in the sediment surface (Supplementary file 3). Generally, the measured phenotypic traits of *M. vocator* showed a clear directional variation from urban to wild forests. Females from the Urban forest reproduced through a significantly wider size range (10.58 mm ± 0.79; mean ± SE) than females from the Rural (8.95 mm ± 1.57) and Wild forest (6.44 mm ± 1.17) (Table 1, Fig. 3). Regarding maximum body size, there were significant differences between mangrove types for males and females (Table 1, Fig. 4). However, while male size decreased consistently from urban to wild forests, females showed a different pattern: they were
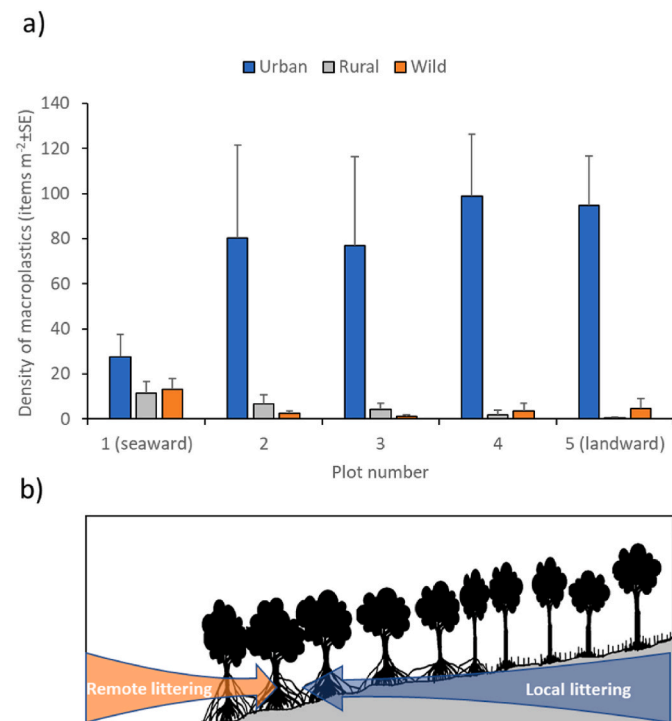
Table 1

Results of the Kruskal-Wallis tests and effect size on the differences in female reproductive lifespan and maximum sizes for male and female *Minuca vocator* among forest types (urban, rural and wild forests). Significant factors (α = 0.05) are highlighted in bold.

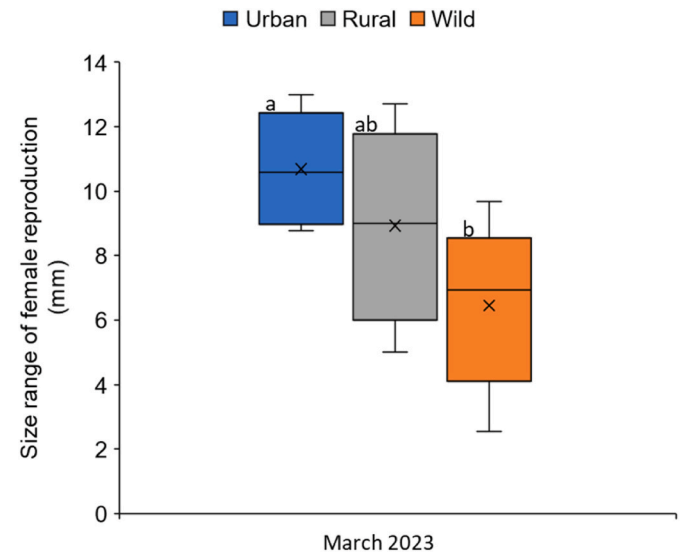| Phenotypic trait	Factor	χ^2	gl	p	ε^2
Reproductive lifespan	Forest type	6.80	2	0.033	0.523
Maximum size (male)	Forest type	12.5	2	0.002	0.169
Maximum size (female)	Forest type	11.6	2	0.003	0.170

Fig. 3. Boxplot on the variability in the size range of female reproduction of *Minuca vocator* among urban (Turbo bay) rural (El Uno bay) and wild (Coquito point) mangrove forests from the Urabá Gulf, Colombian Caribbean. Box plots show: 75% percentiles, x: mean, line median, error bars: max-min. Forest types with different letters indicate significant differences in the mean rank after Dwass-Steel-Critchlow-Fligner tests. No outliers were excluded for figures or statistic tests.

smaller in the Rural forest, compared with females in the Urban and Wild forest. In turn, body condition of male and female crabs in the Urban and Rural forest were significantly higher than that in the Wild forest (Table 2, Fig. 5).

3.3. Female fecundity through age intervals

The comparison of the relationship between female fecundity and age between the Urban and Wild forests changed through time (Fig. 6). In March, although female crabs from the Urban forest showed higher fecundity through age, the slopes were not statistically different (Student's *t*-test, t = 0.42, df = 20, p = 0.673). In April, female fecundity was slightly higher for the Wild forest, but the observed difference between slopes was not significant (Student's *t*-test, t = 0.21, df = 20, p = 0.834). In contrast, during May female crab fecundity was clearly higher in the Urban forest (Student's *t*-test, t = 3.19, df = 21, p = 0.004). Therefore, if the regression model properly represents the lifetime reproductive success of an average female in the population, there were statistical differences only in May 2022, with females in the Urban forests showing higher reproductive success.

3.4. Female survival

The size frequency distributions shown in Fig. 7 showed fundamental differences, suggesting that female survival was lower in wild mangroves. First, urban crab populations more male-dominated; the male-
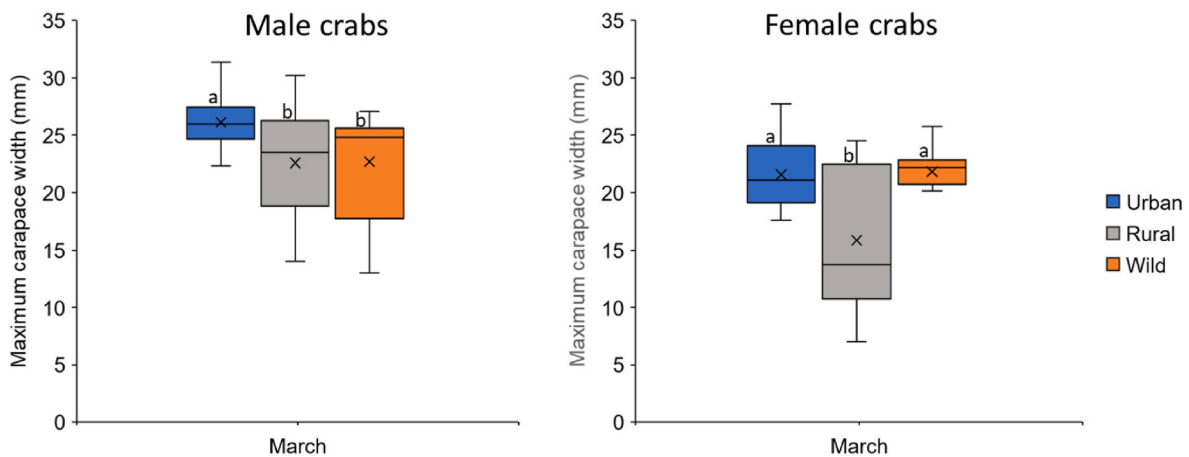

Fig. 2. a) Spatial variability in the mean density of macroplastic litter in surface sediments in urban (Turbo bay) rural (El Uno bay) and wild (Coquito point) mangrove forests from the Urabá Gulf, Colombian Caribbean. Error bars are the standard error. b) schematic model of a mangrove forests profile showing the sieve effect of mangrove roots on local littering (urban mangroves) versus remote littering (wild mangroves) (see discussion).

Fig. 4. Boxplots on the variability in maximum body size of male (left panel) and female (right panel) *Minuca vocator* among urban (Turbo bay) rural (El Uno bay) and wild (Coquito point) mangrove forests from the Urabá Gulf, Colombian Caribbean. Box plots show: 75% percentiles, x: mean, line median, error bars: max-min. Forest types with different letters indicate significant differences in the mean rank after Dwass-Steel-Critchlow-Fligner tests. No outliers were excluded for figures or statistic tests.

Table 2
Results of ANOVA analysis on the differences in body condition (scaled-body condition index) among forest types (urban, rural and wild forests) for male and female *Minuca vocator*. Significant factors ($\alpha = 0.05$) are highlighted in bold.

	Source	df	SS	MS	F-value	P
Males	Forest type	2	4.70	2.34	16.32	<0.001
	Residuals	323	46.47	0.14		
Females	Forest type	2	3.05	1.52	19.61	<0.001
	Residuals	205	15.91	0.07		

to-female ratio in the urban mangrove was higher (2.20 ± 0.22) than in the wild mangrove (1.49 ± 0.26). Second, although females (ovigerous and non-ovigerous) reached slightly larger sizes in the urban mangrove, ovigerous females were less abundant in the urban mangrove ($9.75\% \pm 2.54$) compared to the wild mangrove ($14.62\% \pm 0.86$). Third, the highest frequencies of females in the urban mangrove occurred in the medium size range (14–19 mm), while in the wild mangrove they occurred in the large size range (19–24 mm).

4. Discussion

4.1. Density of macroplastic litter in urban versus wild mangrove forests

Our results largely confirm that (i) mangrove forests, particularly those surrounding cities, act as sinks for macroplastic pollution, (ii) landward areas within mangroves accumulate higher loads of plastics. The observed mean density of macroplastics in rural (4.86 ± 1.57 items m^{-2}) and wild (5.00 ± 1.59 items m^{-2}) mangrove forests are similar to the mean density (6.45 ± 3.04 items m^{-2}; Table 1) of anthropogenic marine litter from different mangrove forests (see review by Luo et al., 2021). Despite high variability, mangrove forests are more effective traps for anthropogenic materials in comparison with other coastal ecosystems (Martin et al., 2019; Martin et al., 2020; Luo et al., 2021). Indeed, as observed here, comparative studies show that the mean density of macroplastics in urban areas may be one or two orders of magnitude higher than that in less developed areas (Riascos et al., 2019; Chee et al., 2020).

On the other hand, we found that landward zones retain more plastic items than seaward zones in urban mangroves but the opposite is true in rural and wild forests. This more likely reflect the mixed source of litter pollution (local or remote i.e., driven by tidal flushing from elsewhere; see Fig. 2b) characterizing urban mangroves versus the remote source of
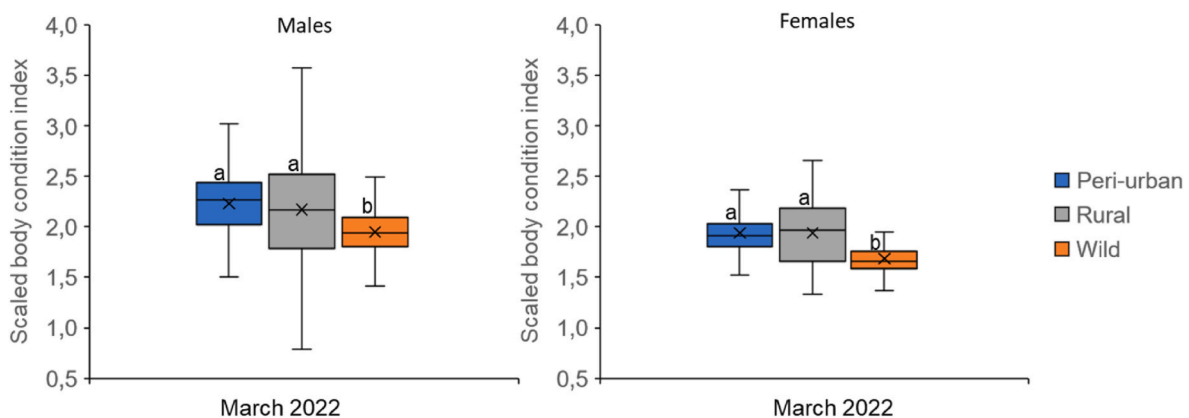

Fig. 5. Changes in scaled body condition index along the urban-wild gradient. Boxplots on the variability in scaled-body condition index of male (left panel) and female (right panel) *Minuca vocator* among urban (Turbo bay) rural (El Uno bay) and wild (Coquito point) mangrove forests from the Urabá Gulf, Colombian Caribbean. Box plots show: 75% percentiles, x: mean, line median, error bars: max-min. Forest types with different letters indicate significant differences in the mean rank after Dwass-Steel-Critchlow-Fligner tests. Note that Y-axis was cut for better visualization; no outliers were excluded for figures or statistic tests.
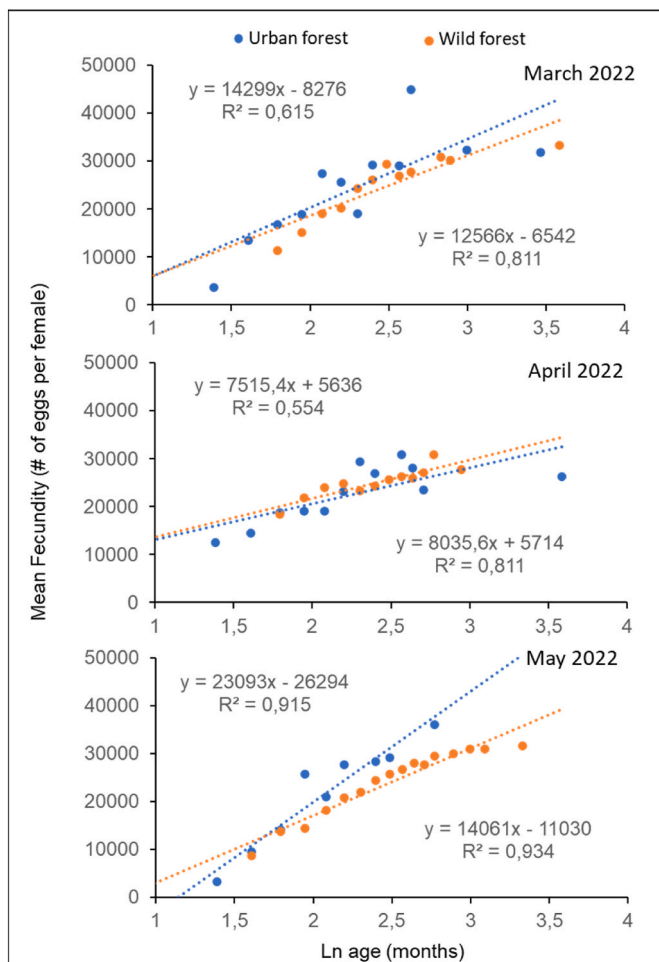
Fig. 6. Variability in fecundity of female *Minuca vocator* as a function of ln-transformed age during three monthly reproductive pulses in urban forests (Turbo bay) and wild forests (Coquito point) from the Urabá Gulf. Ln transformations were performed to linearize age-fecundity relationships. Note that X-axis was cut for better visualization; no outliers were excluded for figures or statistic tests.

pollution prevailing in rural and wild forests. The three-dimensional structural properties of mangrove roots (in our case *Rhizophora mangle* aerial roots and *Avicennia germinans* pneumatophores) exert a sieve effect on plastic materials produced locally or remotely (Luo et al., 2022). These findings, and the fact that only surface plastic litter are usually registered, show that sediments from landward areas in urban mangrove forests are likely the most plastic polluted coastal habitats worldwide. Thus, it is puzzling that burrowing animals are proliferating precisely in these environments.

4.2. The urban crab phenotype

Our results are generally in line with previous studies showing that different species within the family Ocypodidae are able to thrive in highly polluted and modified environments shaped by the urban expansion in different continents (Cannicci et al., 2009; Penha-Lopes et al., 2009a; Costa and Soares-Gomes, 2015). The Urbanization of mangroves represents a natural ecological experiment imposing similar selective pressures and providing similar opportunities, thereby favoring particular phenotypic changes. Our results showed that *M. vocator* generally increased their (female) reproductive lifespan, body size (males) and body condition (both sexes) from wild to urban mangrove forests. We hypothesize that despite the wide array of anthropogenic

disturbances brought about by urbanization, the provision of food subsidies from intensive human activities in urbanized mangroves drive the observed phenotypic changes. Evidence from invertebrates in marine systems is scant, but the synthesis of available evidence shows that the emergence of predictable anthropogenic food subsidies across ecosystems translates into population level changes, including increased body condition, reproductive performance and body size (Oro et al., 2013; Plaza and Lambertucci, 2017; Szulkin et al., 2020). Mangrove trees are often the dominant carbon source to offshore fisheries and inshore consumers in wild forests, with macroalgae, benthic microalgae and seston being secondary sources. However, in urbanized forests about 50% of all carbon available for consumers (including invertebrates and dense bird populations) may originate from predictable anthropogenic subsidies, consisting mainly of organic loading of urban wastewater and agricultural activities (Li and Lee, 1998; Lee, 2000). Fiddler crabs are deposit feeders, they use the setae of the maxilipeds to brush sediment particles and sort their food –microphytobenthos, bacterial films and plant detrital material (Colpo and Negreiros-Franzoso, 2011; Peer et al., 2015). Therefore, these crabs may not feed directly on anthropogenic food. Instead, Penha-Lopes et al. (2009b) suggested that anthropogenic carbon may fuel the increase the abundance of bacteria and microbenthic algae. However, the high spatial-temporal predictability of anthropogenic subsidies may influence foraging activity, dietary patterns and the searching process (Oro et al., 2013). This, and observed shifts to opportunistic generalist feeding behavior in fiddler crabs (Peer et al., 2015; Per. Obs) suggest that *M. vocator* may be feeding directly on anthropogenic food subsidies. Hence, both the disturbances and opportunities created by urban encroachment on mangrove forest surrounding Turbo city during the last two centuries likely shaped a distinctive urban phenotype that may have deep ecological and evolutionary implications.

4.3. Female fecundity and survival

Any directional selection on a given phenotype only make sense in ecological and evolutionary terms if the selected phenotype confers advantage in terms of fitness –survival and reproductive success – (Hendry, 2016). Our results show that a longer reproductive lifespans, larger body sizes and higher body condition characterizing urban phenotypes not necessarily translate into increased reproductive success as we hypothesized. A significantly higher slope of the relationship between fecundity and age in the urban mangrove was only observed in May. One could argue that this short-term increase in fitness *per capita* may be still important from a population perspective. But this is seemingly not the case; the observed changes in size structure strongly suggest that female survival is lower in urban settings, thus hindering fitness. In fact, fecundity in the urban mangrove was only significantly higher in May, coinciding with the lowest abundance of ovigerous females. We argue that a reasonably explanation for a lower survival would be an increased predation pressure in urban versus wild forests, for the following reasons. Fiddler crabs have long been quintessential examples of male-biased sex ratios. First, a meta-analysis of this widespread feature suggested that male-biased sex ratios in fiddler crab populations result from increasing predation on female crabs during the ontogeny; *i.e.* biased sex ratios are acquired through post-recruitment processes (Johnson, 2003). Second, dense and diverse bird communities arise as top consumers in urbanized mangrove forests, and they heavily rely on benthic invertebrates being able to proliferate in these human-dominated systems (Li and Lee, 1998). Bird predators may display consistent patterns of sex-biased predation on fiddler crabs. For example, the white ibis (*Eudocimus albus*) chose female or declawed male fiddler crabs (*Uca pugilator*) four times as often as intact male crabs, suggesting that sexual dimorphism substantially affect the vulnerability to avian predators (Bildstein et al., 1989). Moreover, we must keep in mind that wildlife living in the city must cope with novel assortments of environmental conditions that may be stressful (Szulkin et al., 2020),
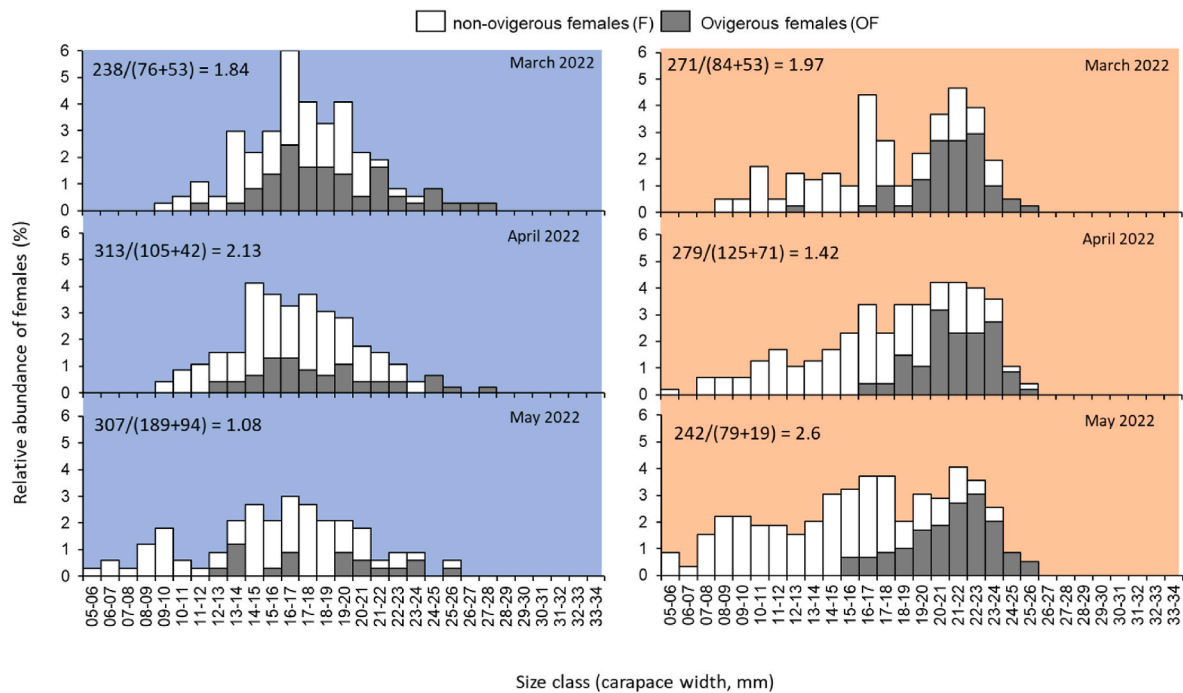
Fig. 7. Temporal changes in the relative abundance of body sizes of non-ovigerous and ovigerous females of *Minuca vocator* in urban forests (Turbo bay, blue panel) and wild forests (Coquito point, orange panel) from the Urabá Gulf. The numbers in the upper left corner in each plot correspond to the number of males in the numerator, the number of non-ovigerous female and ovigerous females in the denominator and the resulting male-to-female sex ratio for each month and each forest type. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hence imposing additional energetic costs on reproduction.

The selection of urban phenotypes of *M. vocator* does not appear to confer consistent advantages in terms of fitness. However, the fact that similar phenotypic variations have been observed in fiddler crab populations thriving in different urban settings (Brazil, Mozambique, Kenya) should be regarded as ongoing, parallel experiments of local adaptation to the chronic exposure to the wide array of human disturbances in urban mangrove forests. Whiter or not any of these experiments may result in urban speciation depend mainly on the crab species, the balance between dispersal and local adaptation and the time of exposure, a rarely acknowledged factor in urban ecology (Szulkin et al., 2020).

5. Concluding remarks

Our results confirm that urban mangrove forests are effective traps for plastic litter, and therefore are of paramount importance to advance our knowledge of the ecological consequences of increasing levels of plastic littering foreseeable in mangrove forests.

Human disturbances, particularly the availability of anthropogenic food subsidies, linked to the expansion of Turbo city (established in 1840) into mangrove forests, likely foster the development urban *M. vocator* displaying distinctive phenotypic traits. Short pulses of increased individual fitness were obliterated by a reduced survival of female crabs in urban settings, probably hinting at higher predation risk. However, the emergence of fiddler crab populations exhibiting similar phenotypic features in disparate human-dominated systems likely represents parallel experiments of local adaptation.

6. Author contributions

All authors contributed to the study conception and design. Funding acquisition was in charge of J.M. Riascos. Field work was conducted by N. Gomez and J.M. Riascos. Sample processing, material preparation, data collection, curation and analysis were performed by N. Gomez and

J.M. Riascos. The first draft of the manuscript was written by J.M. Riascos and both authors commented on previous versions of the manuscript and approved the final version.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Universidad de Antioquia funded this work.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2023.122254.

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