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Benthic functional diversity as a valuable tool to identify vulnerable mangrove forests

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ABSTRACT

Mangrove forests are biodiverse systems that harbour a plethora of highly specialised species. The size of a mangrove forest can influence its biodiversity, but the relationship between these two characteristics is not always linear. In the present study, carried out in 36 medium- to small-size mangrove patches across Hong Kong, we determined the size of each mangrove stand, its taxonomic richness, and the functional diversity, redundancy and vulnerability of crab assemblages, to identify those that were more at risk of functional loss. Eight sites displayed a combination of critically low levels of functional richness, functional redundancy and high functional vulnerability. These sites have either lost some of its ecosystem functions or are at risk of losing them. We also highlighted five sites in good condition that could potentially act as reservoirs or supply sites for nearby threatened locations, and that should be the focus of conservation efforts. Our data show that species composition, diversity and functional role of the associated fauna plays a more important role than size in the functioning of such ecosystems. We then simulated the local extinction of eight crab species in light of future climate change and recalculated the previous functional analyses. Our analyses show that the adopted functional indices are effective in comparing the functionality of mangroves at local scales and determining their degradation. Such indices, however, were less reliable for predicting future trends in functionality of the studied mangrove forests, due to lack of long-term datasets and shifted baselines.

1. Introduction

Mangrove forests are critical ecosystems responsible for supporting a wide array of biodiversity and providing humans with several direct and indirect benefits (Lee et al., 2014). The literal pillars of this ecosystem are mangrove plants, tropical and subtropical salt-tolerant trees and shrubs that occupy sheltered coastlines worldwide (Giri et al., 2011). Despite relatively low global species diversity, comprising less than 70 plant species from *circa* 20 different families, the distribution of these mangrove plants once covered nearly 200.000 km^2 of the planet (Polidoro et al., 2010). The unique habitat created by mangrove trees constitutes an important nursery ground for several faunal species, directly contributing to the functioning of terrestrial and marine food webs (Meynecke et al., 2007). These forests provide raw material to coastal populations (Barbier, 2007), aid in reducing coastal erosion (UNEP, 2014), and in protection from tropical cyclone surges and tsunami waves (Dahdouh-Guebas et al., 2005).

An estimated 210 million people live in the vicinity of mangroves (i.e. within 10 km) and rely on the ecosystem services they provide (Dahdouh-Guebas et al., 2021; UNEP, 2014). During the 1980′s and 1990′s, however, the area covered by mangrove forests has reduced by 35 % (Polidoro et al., 2010) and continues reducing, although at the less worrying rates of 0.4–2 % per year (Friess et al., 2020). This decline is projected to continue, due to an increase in coastal development alongside the growing impacts from climate change (Friess et al., 2019). With many forests consequently disappearing or ending up as fragments of what they once were, the maintenance of the ecosystem services they provide can no longer be taken for granted (Duke et al., 2007).

Despite their small size, it has been suggested that mangrove forests can still provide important ecosystem services (Curnick et al., 2019) and

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support a consistent array of biodiversity, responsible for maintaining such services (Cannicci et al., 2021). Most research studies tend to focus on the floral component of mangroves to assess the provisioning of ecosystem services, or lack thereof. Floral composition and total area, in fact, are two of the factors that tend to be related to the health of these forests (Duke et al., 1998; Ellison, 2002; Jia et al., 2023). Associated fauna, on the other hand, tend to be less studied, despite their critical role in the maintenance of these services (Lee, 1998; Cannicci et al., 2008; Kristensen, 2008). It has recently been shown that mangroves with reduced diversity of associated fauna are less functional than those with a higher diversity (Cannicci et al., 2021), highlighting the importance of the faunal component in mangrove ecosystem functions.

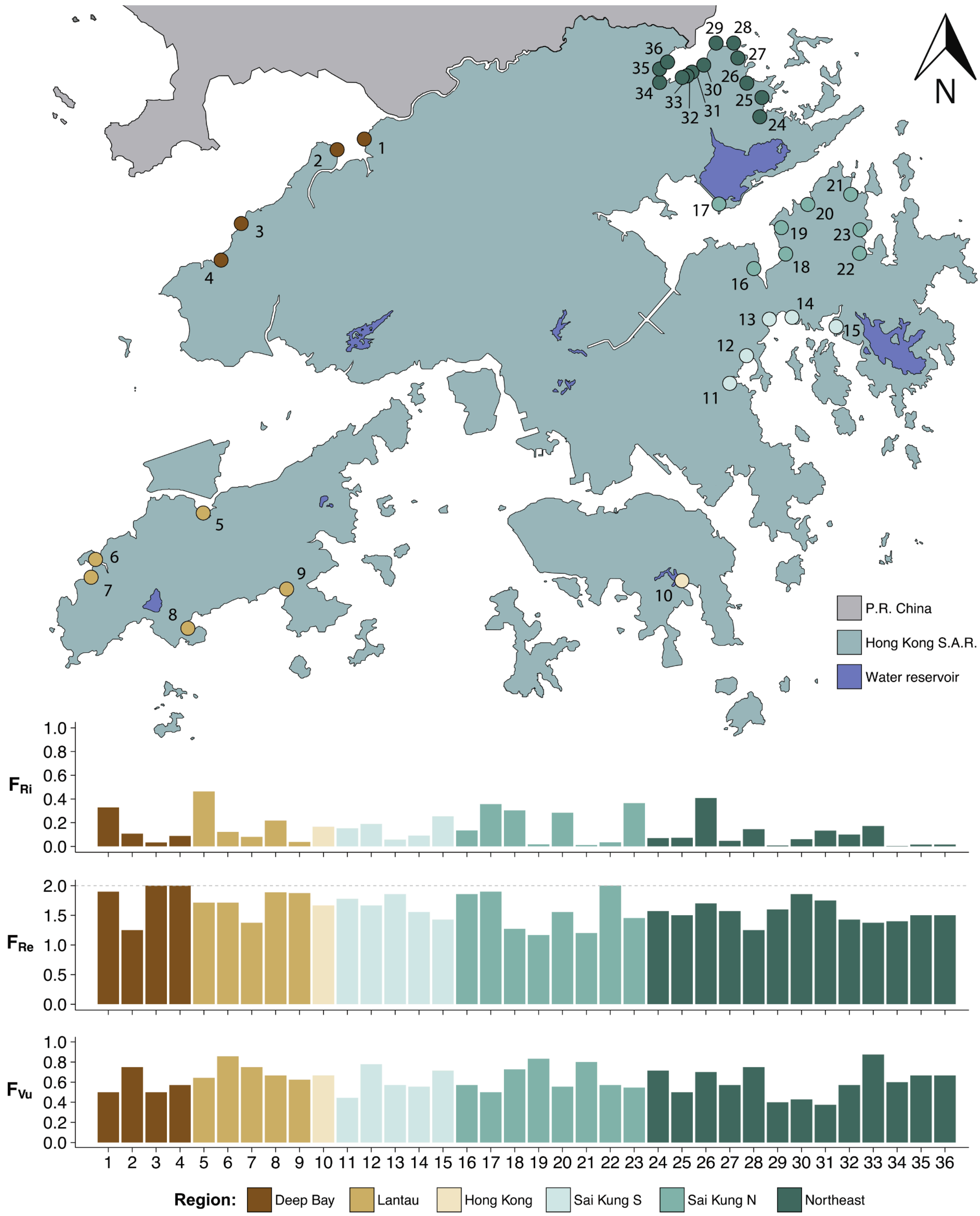

Fig. 1. Map of Hong Kong with the 36 studied sites highlighted with circles of different colours corresponding to six distinct regions. The bar plots depict the results of the three functional indices for the corresponding sites: functional richness (F_{Ri}), functional redundancy (F_{Re}), and functional vulnerability (F_{Vu}). Each bar corresponds to one site (number of the site on the X axis) and they are colour coded based on region. The dashed line above the F_{Re} bar plots represents the minimum number of species necessary (two species) to ensure redundancy. Names of the sites and exact values of the functional indices can be found in Table 1.

The Hong Kong S.A.R. territory (PRC) has experienced a severe reduction in mangrove cover, mainly due to increased coastal development and land reclamation projects (Tam et al., 1997), putting in question the future of mangroves in this densely urbanised place. Despite past and present threats, there are still *circa* 70 mangrove forest patches spread throughout the territory, covering a total area of about 540 ha (Zhang et al., 2021). Hong Kong's mangrove forests host eight native true mangrove species, plus at least two invasive species of the genus *Sonneratia* (Tam et al., 1997), and over 100 associated molluscs and crustacean decapods (Bravo et al., 2021). This high degree of biodiversity of Hong Kong's mangroves, which matches the one observed for other local marine ecosystems, is attributed to the geographical location of this territory, placed in an area that is either the northernmost or southernmost range of distribution limits for several species (Morton and Morton, 1983).

With climate change and urban development threatening the long-term survival of mangrove ecosystems, Hong Kong can provide a window into the future survival of their floral and faunal communities. Assessing the current functionality of Hong Kong's mangroves and predicting the impact of the disappearance of the most vulnerable associated species (e.g. species at the edge of their distribution range) on such functionality, can provide a novel tool to inform future conservation of this threatened ecosystem. Quantifying the functional diversity of the associated fauna is one way of assessing the current, and future, state of these mangroves. The combined use of indices such as Functional Richness (F_{Ri}), Functional Redundancy (F_{Re}), and Functional

Table 1
List of studied sites with their corresponding area (in hectares), region, number of crab species, number of functional entities (FEs), and values of functional richness (F_{Ri}), functional redundancy (F_{Re}), and functional vulnerability (F_{Vu}) at each of the locations. Sites highlighted in green were identified as the top performers in at least two of the functional indices (F_{Ri}, F_{Re} and F_{Vu}). The sites in bold had values in the top quartile in all three indices. Conversely, the sites highlighted in orange were the worst performers from a functional perspective.

Site	Name	Region	Latitude	Longitude	Area (ha)	Crabs	FEs	F_{Ri}	F_{Re}	F_{Vu}
1	**Mai Po**	Deep Bay	22°29'35.7"N	114°01'54.8"E	300.0	19	10	0.33	1.90	0.50
2	Tsim Bei Tsui (Sha Kiu Tsuen)	Deep Bay	22°29'16.24"N	113°59'52.60"E	3.74	10	8	0.11	1.25	0.75
3	Ha Pak Nai (Ap Tsai Hang)	Deep Bay	22°26'22.11"N	113°56'48.61"E	0.85	12	6	0.03	2.00	0.50
4	Ha Pak Nai (near Landfill)	Deep Bay	22°25'30.30"N	113°56'20.05"E	1.23	14	7	0.09	2.00	0.57
5	Tung Chung	Lantau	22°16'50.23"N	113°55'42.88"E	3.86	24	14	0.46	1.71	0.64
6	Hang Mei	Lantau	22°15'08.09"N	113°52'05.46"E	2.50	12	7	0.12	1.71	0.86
7	Tai O	Lantau	22°14'56.91"N	113°51'47.43"E	9.69	11	8	0.08	1.38	0.75
8	Shui Hau	Lantau	22°13'09.00"N	113°55'08.20"E	0.90	17	9	0.22	1.89	0.67
9	Pui O Wan	Lantau	22°14'25.00"N	113°58'49.13"E	0.20	15	8	0.04	1.88	0.63
10	Tai Tam	Hong Kong	22°14'44.83"N	114°13'23.16"E	0.20	15	9	0.17	1.67	0.67
11	Ho Chung	Sai Kung S	22°21'15.76"N	114°15'08.97"E	2.37	16	9	0.15	1.78	0.44
12	Che Keng Tuk	Sai Kung S	22°22'19.37"N	114°15'49.30"E	0.71	15	9	0.19	1.67	0.78
13	Tai Wan	Sai Kung S	22°23'40.49"N	114°16'44.96"E	0.48	13	7	0.06	1.86	0.57
14	Wong Chuk Wan	Sai Kung S	22°23'43.19"N	114°17'05.96"E	0.83	14	9	0.09	1.56	0.56
15	Wong Yi Chau	Sai Kung S	22°23'19.95"N	114°19'11.72"E	0.25	10	7	0.25	1.43	0.71
16	Sai Keng	Sai Kung N	22°25'16.76"N	114°16'07.14"E	6.66	13	7	0.13	1.86	0.57
17	**Ting Kok**	Sai Kung N	22°28'23.1"N	114°12'51.1"E	8.77	19	10	0.36	1.90	0.50
18	Yung Shue O	Sai Kung N	22°25'33.02"N	114°17'14.81"E	1.85	14	11	0.30	1.27	0.73
19	**Sham Chung**	Sai Kung N	22°26'32.47"N	114°17'03.31"E	0.16	7	6	0.02	1.17	0.83
20	Lai Chi Chong	Sai Kung N	22°27'16.27"N	114°18'02.78"E	0.19	14	9	0.28	1.56	0.56
21	**Hoi Ha Wan**	Sai Kung N	22°27'40.00"N	114°19'37.55"E	0.10	6	5	0.01	1.20	0.80
22	To Kwa Peng	Sai Kung N	22°25'43.39"N	114°20'00.84"E	1.74	14	7	0.03	2.00	0.57
23	Tai Tan	Sai Kung N	22°26'20.42"N	114°19'59.12"E	1.15	16	11	0.37	1.45	0.55
24	Sam A Chung	Northeast	22°30'27.50"N	114°16'24.26"E	1.03	11	7	0.07	1.57	0.71
25	Sam A Tsuen	Northeast	22°30'56.06"N	114°16'17.40"E	0.85	9	6	0.07	1.50	0.50
26	Lai Chi Wo	Northeast	22°31'33.89"N	114°15'44.92"E	1.91	17	10	0.41	1.70	0.70
27	So Lo Pun	Northeast	22°32'16.85"N	114°15'22.23"E	1.17	11	7	0.05	1.57	0.57
28	Yung Shue Au II	Northeast	22°31'54.56"N	114°14'08.80"E	0.47	10	8	0.15	1.25	0.75
29	Yung Shue Au	Northeast	22°32'40.03"N	114°14'49.78"E	0.78	8	5	0.01	1.60	0.40
30	Kuk Po	Northeast	22°32'41.64"N	114°15'13.57"E	1.96	13	7	0.06	1.86	0.43
31	Fung Hang II	Northeast	22°31'48.59"N	114°13'38.76"E	0.16	14	8	0.13	1.75	0.38
32	Fung Hang	Northeast	22°31'41.42"N	114°13'17.65"E	0.10	10	7	0.10	1.43	0.57
33	Kai Kuk Shue Ha	Northeast	22°31'34.80"N	114°13'10.45"E	0.38	11	8	0.17	1.38	0.88
34	Nam Chung	Northeast	22°31'32.52"N	114°12'29.61"E	1.15	7	5	0.00	1.40	0.60
35	Sha Tau Kok	Northeast	22°32'01.79"N	114°12'31.38"E	2.19	9	6	0.02	1.50	0.67
36	Nam Chung II	Northeast	22°31'46.12"N	114°12'24.97"E	8.80	9	6	0.02	1.50	0.67

Vulnerability (F_{Vu}) allows for the identification of forests that are more vulnerable due to a lack of redundancy in functions being performed, or an overabundance of unique functional traits (Mouillot et al., 2014). Conversely, it also aids in the identification of mangrove patches that may act as reservoirs to nearby forests due to their high functional diversity values (Dahdouh-Guebas et al., 2022). This approach also allows for the recognition of species crucial to the functioning of the ecosystem, based on the uniqueness of their traits.

We inferred the above-mentioned functional diversity indices for 36 mangrove forests of different areas within the Hong Kong territory, to assess their ecological degradation and functionality. These indices were estimated from the functional traits of 51 species of brachyuran crabs recorded at each forest. This approach allowed us to: 1) assess whether small mangroves can still be functional; 2) identify forests that are critically degraded and those that may act as reservoirs; 3) study the impact of the disappearance of species potentially threatened by climate change to the functionality of mangroves.

2. Materials and methods

2.1. Study area

This study was conducted at 36 mangrove stands across Hong Kong (Fig. 1). All the selected mangrove stands were smaller than 10 ha (Bravo et al., 2021), with an average size of 1.98 ha and the smallest not going above 0.1 ha (Table 1). Most of these forests kept shrinking in area until the end of the last century, remaining stable, or slightly increasing in size over the last two decades (Tam et al., 1997, Zhang et al., 2021). The only exception in our dataset is Mai Po Forest Reserve, a protected Ramsar site that consistently increased in area and remains the largest mangrove patch in the Greater Bay Area, at 300 ha. The majority of the stands (72 %) were located on the eastern coast of Hong Kong, exposed to oceanic conditions with higher salinity and lower nitrogen concentrations. Conversely, the stands on the western coast, including Mai Po, were exposed to the Pearl River estuary that discharges water characterised by low salinity, and high sedimentation and nutrient loads (Duprey et al., 2016).

2.2. Field surveys

To assess mangrove crab diversity, we conducted extensive field surveys in each of the 36 studied sites (Fig. 1) between 2017 and 2020, predominantly between June and September, when crabs are known to be more active (Morton and Morton, 1983; Poon et al., 2010). We focused on mangrove crab communities for two main reasons. The first is related to their role as major ecosystem engineers (Kristensen, 2008) and their renowned role in nutrient cycling, organic matter processing, soil bioturbation and aeration, which ultimately result in mangrove tree growth, primary production, and recruitment (Lee, 1998; Cannicci et al., 2008, 2021). The second reason is related to the fact that we could base our assessment on an updated and comprehensive taxonomic knowledge of Hong Kong brachyuran crabs' diversity (Bravo et al., 2021; Wong et al., 2024), while such detailed knowledge is not available for other components of Hong Kong mangrove macrofauna. The surveys were carried out by a minimum of two researchers during both low spring and neap tides and lasted from 30 min to two hours, depending on the size of the mangrove site. All sites were investigated multiple times, both during the day and at night to account for the variability in the activity of different species. The surveys were carried out moving from the landward to the seaward side, with all possible microhabitats (sediment, rocks, debris, tree barks, roots, canopy, and litter) being routinely checked for the presence/absence of different crab species. Due to the number of sampled sites and of temporal replicates needed to assess the diversity of crab communities at the different sites, only the presence/absence of crab species was recorded at each site.

Voucher specimens for all crab species were collected, preserved in 75 % ethanol and transported to the laboratory for further identification, using the most updated taxonomic literature available. Since the identification to species level was not always possible using exclusively a morphological approach, DNA barcoding was also performed and checked against a DNA barcode library of mangrove crabs in Hong Kong (see Bravo et al., 2021 for DNA barcode library and methodology used).

2.3. Functional indices

To best represent the macrofaunal communities present at the different mangrove stands from a functional perspective, three categorical traits were used: 1) position along the intertidal area; 2) feeding habits; and 3) behavioural traits potentially affecting habitat characteristics. The position along the intertidal zone was coded using five categories: supratidal, intertidal forest, intertidal mudflat, intertidal rocky, and subtidal. Feeding and behavioural traits were coded using a fuzzy logic approach, allowing to categorise species that feed on more than one item. In our case, the fuzzy logic approach never resulted in a species being classified with more than two categories, with the weight being evenly distributed between the two (i.e. 0.5 or 50 % for each of the two categories). The eight feeding habits considered were: detritivore, leaf litter and propagule feeder, fresh mangrove leaves feeder, macroalgal feeder, microalgae and bacteria feeder, omnivore, predator, and scavenger. To further assess the ecological impact of the various species, six behavioural traits were identified, also using a fuzzy logic approach: burrowing, surface digging, free living, fragmenting, leaf storing, and surface bioturbating.

All crab species were then assigned to the different functional categories according to Cannicci et al. (2021) and expanded on in this study using expert knowledge and available literature (see supplementary data for the specific categories allocated to each species, and the R code used to compute the different indices). The unique combination of functional traits resulted in a total of 23 distinct Functional Entities (FEs; used in the estimation of F_{Re} and F_{Vu}). In combination with the presence/absence records obtained for all crab species across all sites, Functional Richness (F_{Ri}), Functional Redundancy (F_{Re}), and Functional Vulnerability (F_{Vu}) were then computed using the same methodology as in Cannicci et al. (2021) and the framework outlined in Magneville et al. (2022). Briefly, F_{Ri} is estimated by plotting the functional traits of each species into a multidimensional space using Gower distance to estimate the distance between traits and to assign them the same weight. A principal component analysis is then used to determine the coordinates of each species with its combination of traits in that multidimensional functional space. F_{Ri} is then estimated by calculating the proportion of the functional space that is occupied by the species — and their functions — present at a site, with high F_{Ri} values indicating that the community in question has a big representation of trait combinations with various species occupying a wide range of niches and performing different functions. F_{Re} and F_{Vu}, on the other hand, do not use a functional space, but represent instead the average proportion of species performing a specific combination of traits (i.e. FE) at a particular site, as suggested by Mouillot et al. (2014). F_{Re} estimates the average number of species performing the FEs recorded at each site, requiring a minimum value of 2 to ensure overall redundancy for the functions present at that site (i.e. two species per FE). F_{Vu} is a metric that estimates the proportion of FEs supported by a single species, with a value of 1 signifying that 100 % of all FEs at a site are supported by a single species. These two metrics were calculated using the following two equations provided by Mouillot et al. (2014):

$$F_{Re} = \frac{\sum_{i=1}^{FE} n_i}{FE} = \frac{S}{FE}$$

$$F_{Vu} = \frac{FE - \sum_{i=1}^{FE} \min(n_i - 1, 1)}{FE}$$

where FE is the total number of functional entities at a location, S is the total number of species at that same location, and n_i is the number of species in functional entity *i*.

Relationships between the different estimated indices (F_{Ri}, F_{Re}, and F_{Vu}) and the total number of crab species found at specific sites as well as the total area of the site (in ha) were then investigated through Akaike's Information Criterion (AIC), and least squares. In most relationships, linear regression models proved to be the best predictors. In some instances, the linear regression was fitted with a logarithmic transformation of the predictor variable to improve model fit.

The values of the three functional indices were then used to detect mangrove stands that are most at risk of ecological collapse. We identified the nine sites that had the lowest F_{Ri} and F_{Re} values (bottom 25 %) and the nine sites that had the highest F_{Vu} values (top 25 %) and reported the sites that performed the poorest in at least two of the indices. The opposite was then done (i.e. top 25 % for F_{Ri} and F_{Re}, and bottom 25 % for F_{Vu}) to identify the sites that had the best functional values in at least two of the indices.

All analyses were conducted in R (v.4.4.1, R Core Team, 2024) using the package *mFD* (v.1.0.7, Magneville et al., 2022) for the estimation of functional indices. Additionally, the following packages were used for data treatment and data visualisation: *dplyr* (v.1.1.4, Wickham et al., 2020), *ggplot2* (v.3.5.1, Wickham, 2016) and *ggpubr* (v.0.6.0, Kassambara, 2020).

2.4. Future predictions

To infer the robustness and usefulness of the functional indices approach to forecast ecosystem functionality in future climate change scenarios, we simulated the consequences of local extinctions of some of the sampled species on the functionality of Hong Kong's mangroves. We postulated that Hong Kong mangroves crab species at the edge of their distribution range would likely be the most susceptible to changes (Sunday et al., 2012). We also hypothesised that species that are at their southernmost limit of their known distribution range in Hong Kong could move northward, seeking a cooler refuge (Hickling et al., 2006). We therefore identified six crab species as potentially most vulnerable to local extinction in Hong Kong: *Chasmagnathus convexus, Chiromantes haematocheir*, *Orisarma dehaani*, *Orisarma intermedium*, *Orisarma neglectum*, and *Sinosesarma tangi* (Wong et al., 2024; see Fig. 2). Because extinction risk is greater in species with smaller geographic ranges (see Tietje et al., 2020), we considered an additional two species, *Haberma tingkok* and *Orisarma patshuni*, which are endemic to Hong Kong, or its immediate vicinity, and have very specific microhabitats (Cannicci and Ng, 2017; Schubart and Ng, 2020). F_{Ri}, F_{Re} and F_{Vu} were then calculated a second time, using the same parameters as the analysis outlined above but excluding these eight crab species from the analysis.

To test for significant differences in the functional diversity indices and number of functional entities before and after the removal of the eight species of crabs, the F_{Ri}, F_{Re}, F_{Vu}, and FE results were tested for normality using a Shapiro-Wilk test. F_{Vu} was normally distributed so a paired *t*-test was conducted afterwards. F_{Ri}, F_{Re} and FE were not normally distributed, therefore, the non-parametric Wilcoxon signed-rank test was used.

3. Results

3.1. Functionality of Hong Kong's mangroves

We recorded a total of 51 species across 36 sites within the Hong Kong territory, totalling 459 occurrences. On average, each site had 12.75 ± 3.8 (mean ± standard deviation) distinct crab species, with Hoi Ha Wan recording the lowest number (six species), and Tung Chung recording the most (24 species). Across the studied mangroves, F_{Ri} and F_{Re} were low, and F_{Vu} was high, indicating the susceptibility of Hong Kong's mangroves to future impacts (Table 1, Fig. 1).

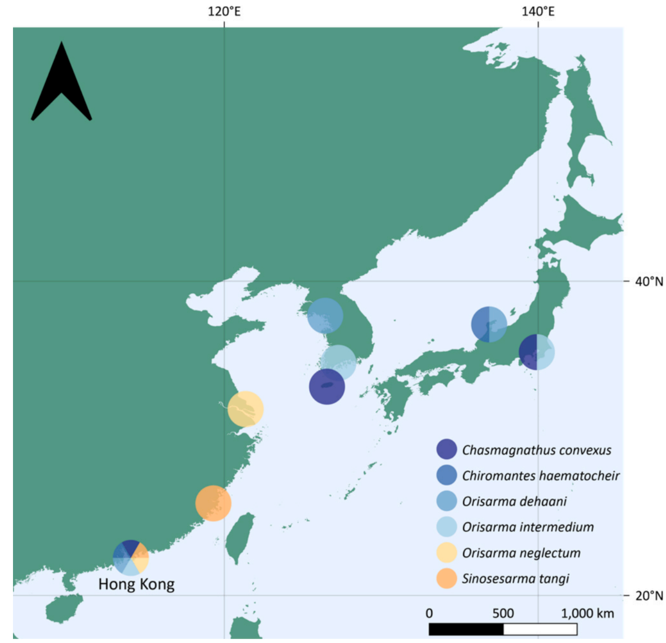

Fig. 2. Map with distribution of the six crab species that have Hong Kong as their southern distribution limit. The semi-circles and full circles represent the northern (known) distribution limits, colour coded based on species, and the pie chart symbolises the shared southern distribution limit for these species in Hong Kong. Some species are represented with more than one northern distribution limit. More details on the literature used to establish these limits and their exact locations can be found in Table S1.

The average F_{Ri} across all sites was 0.14 ± 0.13, with all sites having values below 0.5. Half of the sites had a value of F_{Ri} below or equal to 0.1, and only nine sites (25 % of the total) had values above 0.2. Whilst there were no strong geographical trends, we recorded more sites with very low F_{Ri} on the East compared to the West coast, particularly in the Sai Kung area (Fig. 1).

A total of 23 functional entities (FEs) were identified in this study. The number of FEs varied from five to 14 across the different studied sites (Table 1), with Tung Chung (site 5) having 14 and Hoi Ha Wan, Yung Shue Au, and Nam Chung (sites 21, 29, and 34 respectively) on the lower end of the scale having only five. Twelve FEs were represented by a single species, resulting in no redundancy for more than half of the trait combinations found in Hong Kong mangroves. The FE with most species (eight) was a trait combination of species living in the intertidal mudflat, with a diet of microalgae-bacteria and that were surface bioturbators.

Functional redundancy was low across most of Hong Kong's mangroves included in this study, with an average of 1.61 ± 0.24. A very small proportion of sites (three) had an F_{Re} of 2, with the remainder 92 % of sites (33 sites) having values below 2 with the lowest F_{Re} found in our study being 1.17 for Sham Chung (site 19). In this mangrove site there were six FEs being assured by seven species.

Functional vulnerability displayed values ranging from 0.38 for Fung Hang II (site 31) and 0.88 for Luk Keng (site 33), both sites located adjacently to each other. The average value across the 36 studied sites was 0.63 ± 0.13, meaning that almost two thirds of all FEs are supported by a single species. There were also no discernible patterns of vulnerability in terms of geographic location, with sites being equally affected.

A clear linear relationship between number of crab species and F_{Ri} was observed ($p < 0.001$, $R^2 = 0.59$; Fig. 3A), as well as a moderate asymptotic relationship between F_{Re} and number of crab species ($p < 0.001$, $R^2 = 0.41$; Fig. 3B). All the other investigated relationships, including those of functional indices with each other and with mangrove site area, were either weak or not-significant (Fig. 3C-F).

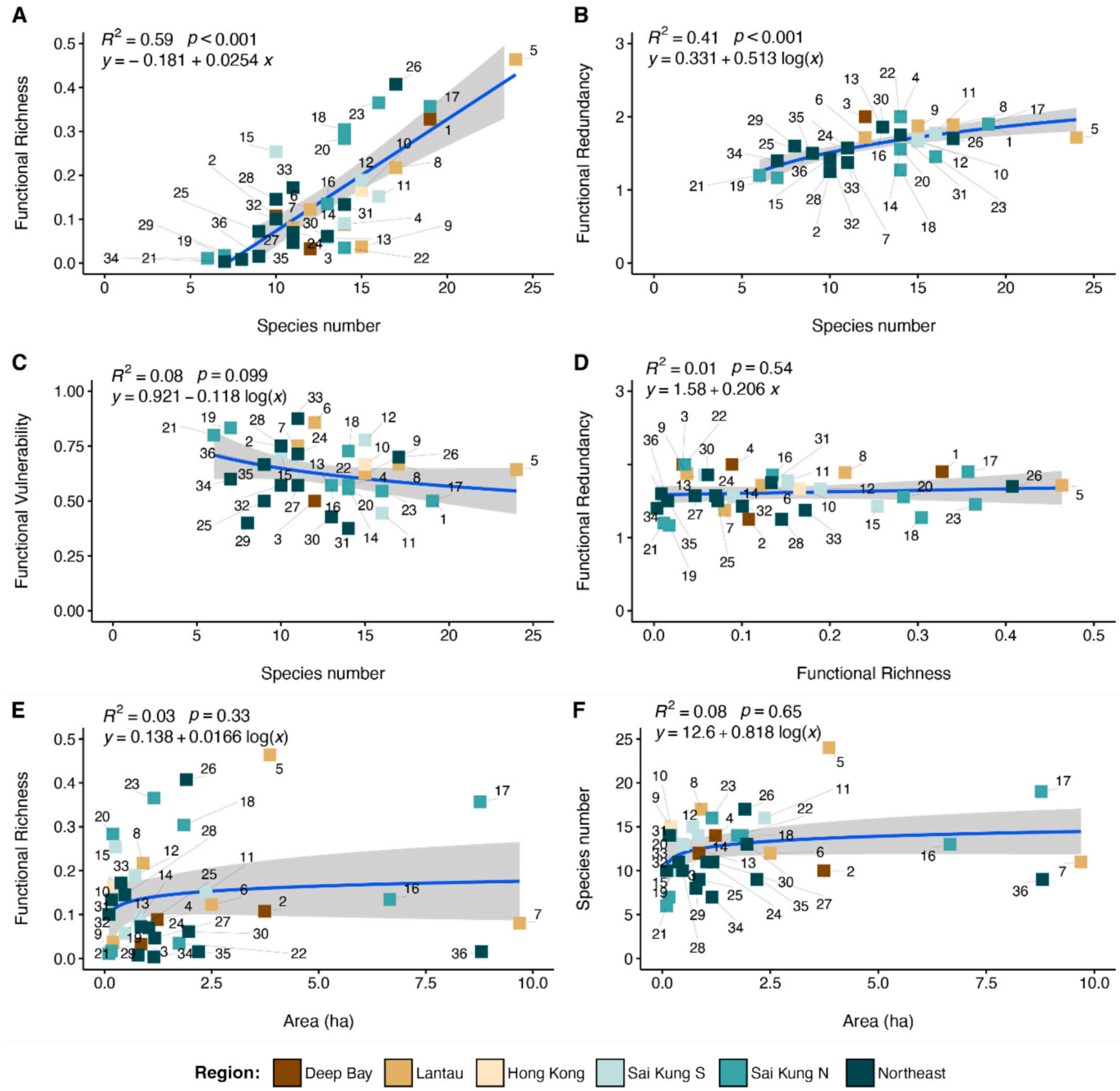

Fig. 3. Relationships between number of crab species recorded, area (in hectares), and the computed functional indices across the 36 studied sites investigated through linear models (see Fig. 1 and Table 1 for key to locations). Best-fit trend lines (blue line) with corresponding standard error (SE) in shaded grey, and the associated R^2 value are shown for: (A) F_{Ri} and species number with a linear trend line; (B) F_{Re} and species number with a logarithmic trend line; (C) F_{Vu} and species number with a logarithmic trend line; (D) F_{Re} and F_{Ri} with a linear trend line; (E) F_{Ri} and area with a logarithmic trend line; and (F) species number and area with a logarithmic trend line. Mai Po (site 1) was removed from plots E-F for better visualisation. Site numbers pointing to the same square signify an overlap in results. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Identification of endangered and functional mangrove sites

We used the bottom quartile for F_{Ri} (sites with values below 0.05) and F_{Re} (sites with values below 1.43), and the top quartile for F_{Vu} (sites with values above 0.72), as indicators of sites that had poor functional performance (highlighted in dark blue in Fig. 4). Any sites that were present in at least two of the aforementioned quartiles were deemed to be particularly at risk of losing functionality. Eight sites fell within this category, with two of them (Sham Chung and Hoi Ha Wan) present in all three of the worst performing quartiles, having an extremely low functional richness and redundancy, and some of the highest functional vulnerability values.

We also estimated the sites that recorded the best functional values using the opposites quartiles (i.e. top quartiles for F_{Ri} and F_{Re}, and bottom quartile for F_{Vu}). Five sites were identified, with Mai Po and Ting Kok present in all three of the best performing quartiles. These last two sites also had some of the highest number of crab species recorded (both with 19 species, surpassed only by Tung Chung with 24).

3.3. Macrofaunal species loss and its implications for functionality

Only one of the eight species that were removed from the original

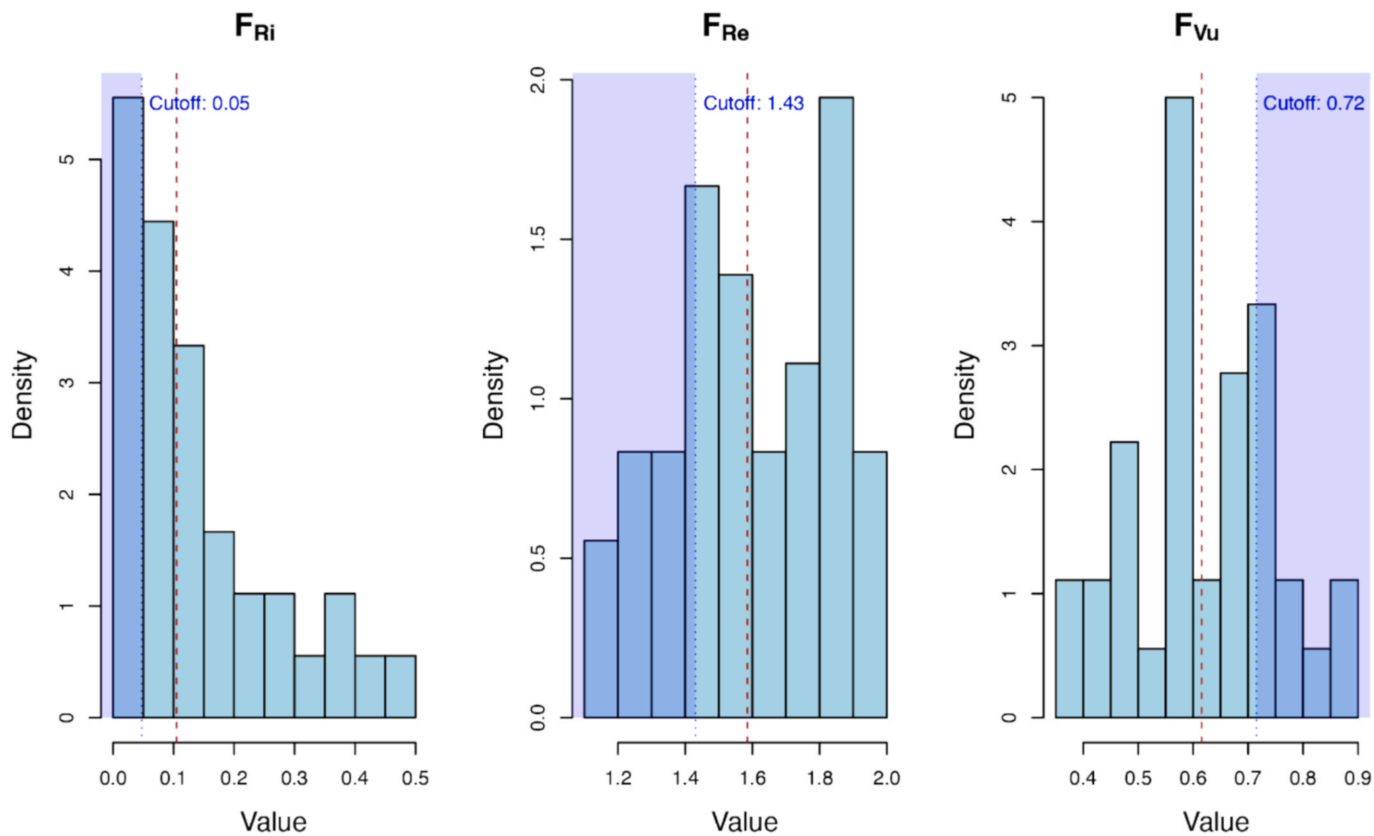

Fig. 4. Three histograms for each of the different functional indices: F_{Ri} on the left-hand side; F_{Re} in the middle; and F_{Vu} on the right-hand side. Each blue-grey bar depicts the number of occurrences (sites) for that specific value of that functional index. The dark shaded blue areas represent values and number of sites in the lowest quartile (i.e. bottom 25 %) for F_{Ri} and F_{Re}, and the highest quartile for F_{Vu} (i.e. highest 25 %). The cutoff values for those quartiles are shown also in blue on the right-hand side of the dotted blue line (which indicates the cutoff limit). These cutoff values were used to identify the "worst functionally performing" sites. To identify the "best performing" ones, the opposite quartiles were used (see end of Section 2.3 for more details). The dashed brown lines represent the median values for each functional index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

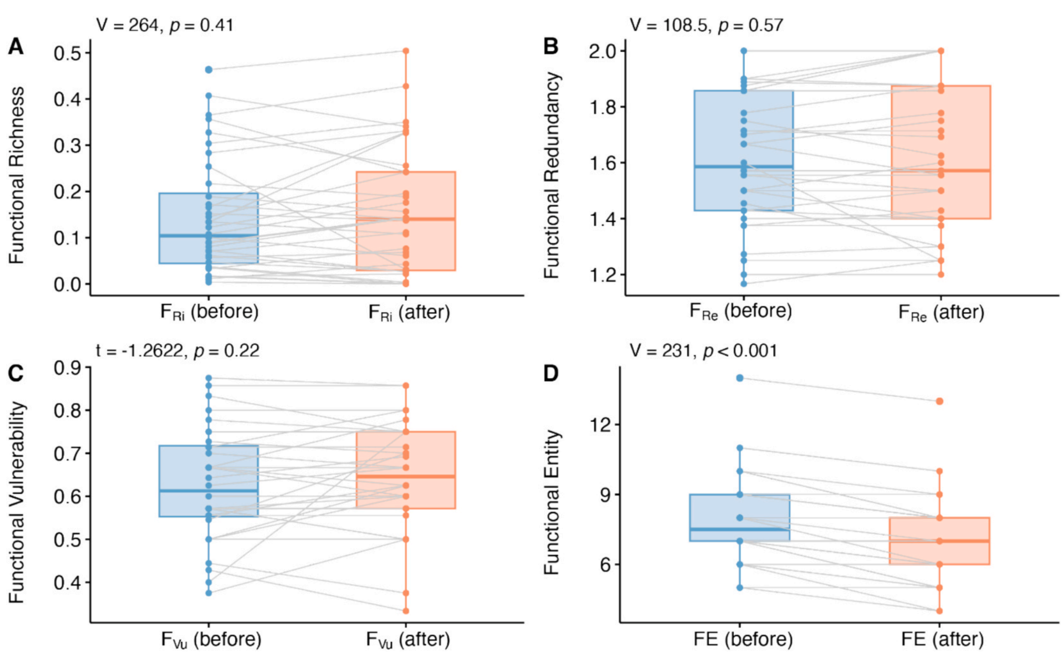

Fig. 5. Boxplots depicting the paired values before (blue) and after (orange) removal of the eight crab species for: (A) Functional richness (F_{Ri}); (B) Functional redundancy (F_{Re}); (C) Functional vulnerability (F_{Vu}); and (D) number of functional entities (FEs). Each coloured dot corresponds to one site, but same number/value results in overlap of sites. The grey lines connect the values belonging to the same site. Results of the pairwise statistical tests are presented in the top left corner of each corresponding plot (see Section 3.3 for more details on the results). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dataset displayed a unique combination of traits. *Haberma tingkok* is the only species that feeds on fresh mangrove leaves, making its combination of traits irreplaceable. *Chasmagnathus convexus*, *Chiromantes haematocheir*, and *Orisarma intermedium* all performed the same combination of traits, but their disappearance resulted in the functional entity they represented to go from one of the most resilient to extinct. The same was true when *Orisarma dehaani* and *O. neglectum* were removed, which caused the extinction of another functional entity. The impact was not as dramatic when *O. patshuni* and *Sinosesarma tangi* were removed, but the functional entity they supported lost half of its representatives, going from four species to two. Most of these species inhabit the supratidal and their disappearance could result in serious functional decline of this zone, going from five FEs supported by 11 species, to three FEs supported by four species.

After the removal of the eight species potentially vulnerable to local extinctions, F_{Ri} remained constant without the presence of these species (Fig. 5, Table S2), going from an average of 0.14 ± 0.13 to 0.15 ± 0.14, and with no significant differences between paired values ($V = 264$, $p = 0.41$). F_{Re} suffered a decline in many sites, but, after such removals, the sites with an F_{Re} equalling 2 increased to seven, suggesting a higher overall amount of redundancy. This increase in redundancy could be seen from the average amount that went up marginally, raising to 1.62 ± 0.27, but not significantly ($V = 108.5$, $p = 0.57$). The number of FEs across the different sites appeared to remain constant, going from a range of 5–14 to one of 4–13 found across the sites. The average number of FEs across the sites reduced by 0.75 resulting in a significant difference between the two analyses ($V = 231$, $p < 0.001$). The total number of FEs also reduced, going from 23 to 20, having now 11 FEs being supported by a single species instead of 12. F_{Vu} remained relatively constant, increasing marginally to 0.64 ± 0.12 but not differing significantly ($t = -1.2622$, $df = 35$, $p = 0.22$). The highest vulnerability found for any site went down, with 0.86 being the highest found (site 33), and the lowest vulnerability also decreased, with the new lowest F_{Vu} value found being 0.33 (site 30).

4. Discussion

Our functional approach revealed a low degree of functionality across Hong Kong's mangroves, with most sites showing low functional richness, low functional redundancy and high functional vulnerability. Whilst the number of crab species present can be a predictor for the performance of some indices, area proved not to be a reliable indicator, highlighting the ecological importance of small mangrove stands. Using a combination of functional indices allowed us to determine sites that were particularly vulnerable from a functional perspective, but also those sites that can still act as biodiversity reservoirs. When looking into the future, and from a functional point of view without any *a priori* knowledge, mangrove stands in Hong Kong will not be fairing any worse than presently, suggesting the limitation of these metrics to predict the future functionality of these dynamic systems.

4.1. Hong Kong's mangroves – Present

The overall low levels of functionality found in this study hint at the presence of mangrove stands that are already impacted and might suffer losses in functional roles soon. The functional richness across Hong Kong's mangroves is not only low, but it is also often supported by rare species with unique traits that tend to be confined to a few sites. This rarity in functional traits was evident from the fact that more than half of all functional entities were supported by a single species, which resulted in low values for functional redundancy and high functional vulnerability. The values of F_{Re} never surpassed 2, indicating a lack of redundancy in functional trait combinations and lack of an "insurance policy", highlighting how unique the roles of crabs in Hong Kong's mangroves are. Crabs are well known bioengineers that play an important role in the environment through oxygenation and bioturbation of the soil (Lee, 1998; Cannicci et al., 2008; Kristensen, 2008). The disappearance of these ecosystem engineers could result in the loss of critical functions for the ecosystem (Dahdouh-Guebas and Cannicci, 2021). Their monitoring can act as a proxy of ecosystem health and should be considered in future conservation and restoration projects (Dahdouh-Guebas et al., 2022).

The positive correlation between species biodiversity and ecosystem functions is a well-established fact in ecology (Cardinale et al., 2006; Duncan et al., 2015) and Hong Kong's mangroves are no exception. Our data shows that the diversity in mangrove associated fauna is a reliable indicator of ecosystem functioning, and new monitoring tools (e.g. environmental DNA metabarcoding) based on DNA barcoding are likely to make this task easier in the future (Bravo et al., 2021). In general, the presence of more species is expected to result in a bigger suite of functional roles and traits, but for mangrove ecosystems this linear relationship has been shown to eventually reach a plateau when more species are considered (Cannicci et al., 2021), similarly to the trend found here for F_{Re} (Fig. 3B). Due to such ecological properties, the use of taxonomic diversity to evaluate the functionality of mangrove systems might not provide a complete and accurate picture, either inflating functional diversity indices because of unknown redundancy in traits, or by overlooking rare and unique traits.

The presence/absence of associated fauna is related to the different types of habitats present at a site. An ecosystem characterised by different patches of sediment types, by different species of trees, and different elevations, will provide many distinct niches and will be more complex, attracting a bigger suite of species (Nauta et al., 2023). In Hong Kong, the sites with the highest F_{Ri} values were usually characterised by having a large sandy area, a forest cover with a relevant tree species diversity, and a rocky part at the back of the mangrove forest with a stream going through the forest. A site with a low F_{Ri} would be missing one or more of these habitats, resulting in the lack of some species and their associated functions.

Site area was not, however, a reliable predictor of site complexity. Whilst most sites that showed a low or very low level of functional diversity had a reduced area, this was not true for all of them. A small site is likely to provide a small niche variety, but a large area does not, however, automatically ensure a higher degree of complexity and a large number of species and functional diversity (Johnson et al., 2003). As an example, Tsim Bei Tsui (3.74 ha; site 2) and Tai O (9.69 ha; site 7) were two of the largest sites sampled in this study but showed some of the lowest values of F_{Ri} and F_{Re}, and high F_{Vu} values. On the other hand, Tai Tan with a total area size below average (1.15 ha; site 23), displayed the third highest F_{Ri}, and an F_{Vu} below average, suggesting the high degree of functionality present in this site, emphasising the value of small mangrove patches (Curnick et al., 2019). However, the low F_{Re} identified for this site serves as a warning to the high degree of functional traits without redundancy that are at risk of disappearance.

4.2. Endangered and functional sites

Having multiple functional indices enabled us to draw more accurate conclusions regarding the current state of Hong Kong's mangroves. We could highlight those that might be on the verge of functional collapse or, alternatively, be used as reservoirs of macrofauna recruitment to adjacent sites.

As mentioned in the previous section, size was not a predictor of functionality, but Ting Kok and Mai Po, which were identified as the best functionally performing sites in our dataset, were also two of the biggest sites, with the former being home to the endemic *Haberma tingkok* (Cannicci and Ng, 2017), another functionally unique species. The conservation of these sites is therefore of paramount importance for the maintenance of functional mangroves in Hong Kong. Two of the other three remaining sites (Shui Hau and Tai Tan), despite being all below average size, showed high crab species diversity and a large presence of species with unique functional traits. Lai Chi Wo and Tung Chung, despite not having been identified as best performing sites, had the highest values of F_{Ri}, with the latter site having the highest number of crab species recorded in this study (24). This is likely explained by the high habitat complexities found in these sites. The very high values of F_{Vu} of these latter sites, however, indicate the presence of functionally unique species that are more at risk of disappearance, and contributed to them falling outside the top quartile for F_{Re} and the lowest quartile for F_{Vu}.

The two sites (Sham Chung and Hoi Ha Wan) identified as the worst functionally performing across all three indices were also two of the smallest ones. Additionally, Sham Chung has been dammed in the past to transform the wetland into rice paddies (Tam and Wong, 2002), which resulted in a loss of habitat complexity. With the exception of Nam Chung (site 34), which was the only site with an F_{Ri} of 0.0, all the other low performing sites had F_{Vu} values on the higher end of the spectrum on par with the lowest F_{Re} values found. This is a strong indication that many of the crab species found at these sites are unique in their functional trait combination. A small disturbance event (e.g. deforestation, pollution) can prove enough to result in the local extinction of unique species from these sites, resulting in the disappearance of certain ecosystem roles.

There is a possibility that not all crab species were found during our surveys, especially as new species keep being recorded from Hong Kong's mangroves (Jimenez et al., 2024), which would likely lead to different results for the studied functional indices. The inclusion of other indices that consider abundance of species (e.g. functional evenness and functional divergence which can be indicators of how balanced the community and their respective traits are), together with the inclusion of other invertebrate taxa of resident mangrove fauna (such as molluscs, polychaetes and oligochaetes) in functional analyses and approaches, could shed more light into the current functionality of Hong Kong's mangroves.

Lastly, it is important to note that the sites that were identified here as either endangered or on the verge of collapse (Fig. 4, Table 1) are still, as far as we know, performing enough functions to provide critical services to adjacent coastal ecosystems and should nonetheless be preserved.

4.3. Hong Kong's mangroves – Future

Predicting the future of Hong Kong's mangroves from a functionality perspective revealed the importance in having baseline information, as the results obtained showed that functional diversity is not expected to decrease even with the local extinction of *circa* 15 % (i.e. eight species) of the total studied species pool.

Recalculating the three functional indices resulted in the new average values remaining stable or departing from the present-day ones in the opposite direction of what was predicted. F_{Ri} showed a slight increase, which is explained by the lower total number of crab species. With less species, and therefore less trait combinations contributing to the overall functional space, the functional metrics adjust to the new baseline, which makes achieving a higher F_{Ri} more easily attainable. The same is true for F_{Re}, where it is easier to achieve a higher redundancy of traits if there are less specialised species performing unique combinations of traits at any given site. This suggests that with the removal of the eight crab species at risk of local extinction, most of the species present at the sites will consist of generalist species. The number of unique FEs also reduced by one, but it increased in proportion, since there was a decrease in total number of FEs. This change in FEs resulted in the slight increase in F_{Vu}, which is a metric that is particularly susceptible to unique FEs.

Given the marginal change in values, sometimes in the opposite predicted direction, we conclude that functional diversity indices were not able to accurately determine the future functionality of mangrove stands in Hong Kong. The fact that the values did not change considerably should not be interpreted as proof that the studied stands are resilient to local extinction. It should be interpreted as a sign of data deficiency, highlighting the importance of having baseline data and continued monitoring. The lack of historic data can, in fact, result in gross underestimations of degradation, with our current knowledge being rooted on already impacted ecosystems (Knowlton and Jackson, 2008). The logistical (Reis-Filho et al., 2020) and taxonomic difficulties (Bravo et al., 2021) presented with regularly sampling the fauna present in mangrove forests results in a lack of long-term, fine scale datasets, and therefore, of baseline information. If regular monitoring does not commence soon, it is likely that we will miss out on local extinctions of fauna and flora, and consequent loss of system functionality going unrecorded. In places that have limited amounts of mangrove forests, such as Hong Kong, this loss could be even more pronounced.

5. Conclusion

In a time where many natural coastal environments are giving way to urban development, the preservation of functional patches is of paramount importance to ensure the long-term functionality of ecosystems. In this study we provided an approach to assess and measure the current degree of functions being performed by mangrove-associated fauna as a proxy of functionality of different sized mangrove forests. With this approach we were able to identify sites that are particularly at risk and sites that could act as biodiversity and functional reservoirs. We showed that small mangrove forests can support relatively high degrees of functionality, and that low functional diversity does not discriminate based on size, with small and big mangrove forests being equally affected. Our study also highlighted the importance of long-term baseline information, so we can accurately record what we might be losing before it is too late.

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CRediT authorship contribution statement

Henrique Bravo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Christine L.Y. Cheng:** Writing – review & editing, Data curation. **Sara Fratini:** Writing – review & editing, Writing – original draft, Supervision. **Pedro Julião Jimenez:** Writing – review & editing, Data curation. **Stefano Cannicci:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

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.

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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.2025.114225.

Data availability

The data used in this study and the R code employed for the computation of the functional indices are available from the following online Zenodo repository: https://doi.org/10.5281/zenodo.17090717

References

Barbier, E.B., 2007. Valuing ecosystem services as productive inputs. Econ. Policy 22 (49), 177–229.

Bravo, H., Cheng, C.L.Y., Iannucci, A., Natali, C., Quadros, A., Rhodes, M., Yip, M.M.L., Cannicci, S., Fratini, S., 2021. A DNA barcode library for mangrove gastropods and crabs of Hong Kong and the Greater Bay Area reveals an unexpected faunal diversity associated with the intertidal forests of Southern China. BMC Ecol. Evol. 21 (180), 1–15.

Cannicci, S., Burrows, D., Fratini, S., Smith, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquat. Bot. 89 (2), 186–200.

Cannicci, S., Lee, S.Y., Bravo, H., Cantera-Kintz, J.R., Dahdouh-Guebas, F., Fratini, S., Fusi, M., Jimenez, P.J., Nordhaus, I., Porri, F., Diele, K., 2021. A functional analysis reveals extremely low redundancy in global mangrove invertebrate fauna. Proc. Natl. Acad. Sci. 118 (32), e2016913118.

Cannicci, S., Ng, P.L.K., 2017. A new species of micro-mangrove crab of the genus Haberma Ng & Schubart, 2002 (Crustacea, Brachyura, Sesarmidae) from Hong Kong. ZooKeys 2017 (662), 67–78.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443 (7114), 989–992.

Curnick, D.J., Pettorelli, N., Amir, A., Balke, T., Barbier, E.B., Crooks, S., Dahdouh-Guebas, F., Duncan, C., Endsor, C., Friess, D.A., Quarto, A., Zimmer, M., Lee, S.Y., 2019. The value of small mangrove patches. Science 363 (6424), 15–17.

Dahdouh-Guebas, F., Jayatissa, L.P., Di Nitto, D., Bosire, J.O., Seen, D.L., Koedam, N., 2005. How effective were mangroves as a defence against the recent tsunami? Curr. Biol. 15 (12).

Dahdouh-Guebas, F., Cannicci, S., 2021. Mangrove restoration under shifted baselines and future uncertainty. Front. Mar. Sci. 8, 8–11.

Dahdouh-Guebas, F., Hugé, J., Abuchahla, G.M.O., Cannicci, S., Jayatissa, L.P., Kairo, J. G., Kodikara Arachchilage, S., Koedam, N., Mafaziya Nijamdeen, T.W.G.F., Mukherjee, N., Poti, M., Prabakaran, N., Ratsimbazafy, H.A., Satyanarayana, B., Thavanayagam, M., Vande Velde, K., Wodehouse, D., 2021. Reconciling nature, people and policy in the mangrove social-ecological system through the adaptive cycle heuristic. Estuar. Coast. Shelf Sci. 248 (106942), 1–29.

Dahdouh-Guebas, F., Friess, D.A., Lovelock, C.E., Connolly, R.M., Feller, I.C., Rogers, K., Cannicci, S., 2022. Cross-cutting research themes for future mangrove forest research. Nat. Plants 8 (10), 1131–1135.

Duke, N., Meynecke, J., Dittmann, S., Ellison, A., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K., Field, C., Koedam, N., Lyee, S., Marchand, C., Nordhaus, I., Dahdouh-Guebas, F., 2007. A world without mangroves? Science 317 (July), 41–43.

Duke, N.C., Ball, M.C., Ellison, J.C., 1998. Factors influencing biodiversity and distributional gradients in mangroves. Glob. Ecol. Biogeogr. Lett. 7 (1), 27–47.

Duncan, C., Thompson, J.R., Pettorelli, N., 2015. The quest for a mechanistic understanding of biodiversity–Ecosystem services relationships. Proc. R. Soc. B Biol. Sci. 282 (20151348).

Duprey, N.N., Yasuhara, M., Baker, D.M., 2016. Reefs of tomorrow: eutrophication reduces coral biodiversity in an urbanized seascape. Glob. Chang. Biol. 22, 3550–3565.

Ellison, A.M., 2002. Macroecology of mangroves: Large-scale patterns and processes in tropical coastal forests. Trees 16 (2–3), 181–194.

Friess, D.A., Rogers, K., Lovelock, C.E., Krauss, K.W., Hamilton, S.E., Lee, S.Y., Lucas, R., Primavera, J., Rajkaran, A., Shi, S., 2019. The state of the world's mangrove forests: Past, present, and future. Annu. Rev. Env. Resour. 44, 89–115.

Friess, D.A., Yando, E.S., Abuchahla, G.M.O., Adams, J.B., Cannicci, S., Canty, S.W.J., Cavanaugh, K.C., Connolly, R.M., Cormier, N., Dahdouh-Guebas, F., Diele, K., Feller, I.C., Fratini, S., Jennerjahn, T.C., Lee, S.Y., Ogurcak, D.E., Ouyang, X., Rogers, K., Rowntree, J.K., Wee, A.K.S., 2020. Mangroves give cause for conservation optimism, for now. Curr. Biol. 30 (4), R153–R154.

Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Glob. Ecol. Biogeogr. 20 (1), 154–159.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Chang. Biol. 12 (3), 450–455.

Jia, M., Wang, Z., Mao, D., Ren, C., Song, K., Zhao, C., Wang, C., Xiao, X., Wang, Y., 2023. Mapping global distribution of mangrove forests at 10-m resolution. Science Bulletin 68 (12), 1306–1316.

Jimenez, P.J., Chang, K., Shih, H Te, Yasuhara, M., 2024. Confirming the occurrence of two fiddler crabs, *Tubuca dussumieri* (H. Milne Edwards, 1852) and *T. coarctata* (H. Milne Edwards, 1852) (Crustacea: Decapoda: Ocypodidae), in Hong Kong by DNA barcoding and morphology. Zootaxa 5476 (1), 177–191.

Johnson, M.P., Frost, N.J., Mosley, M.W.J., Roberts, M.F., Hawkins, S.J., 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecol. Lett. 6 (2), 126–132.

Kassambara, A., 2020. ggpubr: 'ggplot2' Based Publication Ready Plots. R package version 0.6.0.

Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. 6 (2), 0215–0220.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59 (1–2), 30–43.

Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49 (1907), 335–343.

Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Diele, K., Fromard, F., Koedam, N., Marchand, C., Mendelssohn, I., Mukherjee, N., Record, S., 2014. Ecological role and services of tropical mangrove ecosystems: A reassessment. Glob. Ecol. Biogeogr. 23 (7), 726–743.

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., Villéger, S., 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity. Ecography 2022 (1), 1–15.

Meynecke, J.O., Shing, Y.L., Duke, N.C., Warnken, J., 2007. Relationships between estuarine habitats and coastal fisheries in Queensland, Australia. Bull. Marine Sci. 80 (3), 773–793.

Morton, B., Morton, J., 1983. The Sea Shore Ecology of Hong Kong. Hong Kong University Press.

Mouillot, D., Villeger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., Bellwood, D.R., 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. 111 (38), 13757–13762.

Nauta, J., Lammers, C., Lexmond, R., Christianen, M.J.A., Borst, A., Lamers, L.P.M., van Lavieren, H., Naipal, S., Govers, L.L., 2023. Habitat complexity drives food web structure along a dynamic mangrove coast. Mar. Pollut. Bull. 196, 115597.

Polidoro, B.A., Carpenter, K.E., Collins, L., Duke, N.C., Ellison, A.M., Ellison, J.C., Farnsworth, E.J., Fernando, E.S., Kathiresan, K., Koedam, N.E., Livingstone, S.R., Miyagi, T., Moore, G.E., Nam, V.N., Ong, J.E., Primavera, J.H., Salmo, S.G., Sanciangco, J.C., Sukardjo, S., Yong, J.W.H., 2010. The loss of species: Mangrove extinction risk and geographic areas of global concern. PLoS One 5 (4).

Poon, D.Y.N., Chan, B.K.K., Williams, G.A., 2010. Spatial and temporal variation in diets of the crabs *Metopograpsus frontalis* (Grapsidae) and *Perisesarma bidens* (Sesarmidae): Implications for mangrove food webs. Hydrobiologia 638, 29–40.

R Core Team, 2024. *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.

Reis-Filho, J.A., Giarrizzo, T., Barros, F., 2020. Stationary underwater cameras assess more efficiently clear-water mangrove fish assemblages: A comparison of non-extractive techniques. Mar. Ecol. 41 (4), 1–12.

Schubart, C.D., Ng, P.K.L., 2020. Revision of the intertidal and semiterrestrial crab genera *Chiromantes* Gistel, 1848, and *Pseudosesarma* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), using morphology and molecular phylogenetics, with the establishment of nine new genera and two new species. Raffles Bull. Zool. 68, 891–994.

Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. Nat. Clim. Chang. 2 (9), 686–690.

Tam, N.F.Y., Wong, Y.S., Lu, C.Y., Berry, R., 1997. Mapping and characterization of mangrove plant communities in Hong Kong. Hydrobiologia 352, 25–37.

Tam, N.F., Wong, Y., 2002. Conservation and sustainable exploitation of mangroves in Hong Kong. Trees 16, 224–229.

Tietje, M., Rödel, M.O., Schobben, M., 2020. The effect of geographic range and climate on extinction risk in the deep-time amphibian fossil record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 537, 109414.

UNEP, 2014. *The importance of mangroves to people: A call to action*. van Bochove, J., Sullivan, E., Nakamura, T.(Eds). United Nations Environment Programme World Conservation Monitoring Centre, Cambridge. 128pp.

Wickham, H., 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Wickham, H., François, R., Henry, L., Müller, K., 2020. dplyr: A grammar of data manipulation. R package version 1.1.4.

Wong, K.J.H., Ng, P.K.L., Shih, H.-T., Chan, B.K.K., 2024. The Brachyuran Crabs (Crustacea: Decapoda) of Hong Kong: A historical review and catalogue. Zool. Stud. 63 (38), 1–155.

Zhang, T., Hu, S., He, Y., You, S., Yang, X., Gan, Y., Liu, A., 2021. A fine-scale mangrove map of China derived from 2-meter resolution satellite observations and field data. ISPRS Int. J. Geo Inf. 10 (2), 9–20.