A functional analysis reveals extremely low redundancy in global mangrove invertebrate fauna

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Deforestation results in habitat fragmentation, decreasing diversity, and functional degradation. For mangroves, no data are available on the impact of deforestation on the diversity and functionality of the specialized invertebrate fauna, critical for their functioning. We compiled a global dataset of mangrove invertebrate fauna comprising 364 species from 16 locations, classified into 64 functional entities (FEs). For each location, we calculated taxonomic distinctness (Δ+), functional richness (FRi), functional redundancy (FRe), and functional vulnerability (FVu) to assess functional integrity. Δ+ and FRi were significantly related to air temperature but not to geomorphic characteristics, mirroring the global biodiversity anomaly of mangrove trees. Neither of those two indices was linked to forest area, but both sharply decreased in human-impacted mangroves. About 60% of the locations showed an average FRe < 2, indicating that most of the FEs comprised one species only. Notable exceptions were the Eastern Indian Ocean and west Pacific Ocean locations, but also in this region, 57% of the FEs had no redundancy, placing mangroves among the most vulnerable ecosystems on the planet. Our study shows that despite low redundancy, even small mangrove patches host truly multifunctional faunal assemblages, ultimately underpinning their services. However, our analyses also suggest that even a modest local loss of invertebrate diversity could have significant negative consequences for many mangroves and cascading effects for adjacent ecosystems. This pattern of faunal-mediated ecosystem functionality is crucial for assessing the vulnerability of mangrove forests to anthropogenic impact and provides an approach to planning their effective conservation and restoration.

community ecology | functional redundancy | functional traits | biodiversity | mangrove conservation

Mangrove forests, once dominant intertidal ecosystems in the tropics (1), are disappearing at devastating rates worldwide (2, 3). Estimates of their loss are often uncertain due to the nature of available datasets (4) and the imprecision in determining mangrove area (5), but the current consensus on mangrove loss in the last quarter century ranges between 35 to 86% in the worst affected countries (2). Although recent estimates show a decrease in mangrove deforestation (6), global destruction is still happening, putting mangrove ecosystem functionality and, ultimately, provisioning of ecosystem services at risk (7). As recently reassessed (8), mangroves are unrivaled carbon sinks (9) and often contribute significant carbon and nitrogen to offshore habitats (10). They also act as nurseries for species from connected ecosystems (11) and protect tropical coasts from erosion (12) as well as extreme events (13).

As theoretical and empirical studies have shown (14, 15), species extinctions in natural ecosystems often lead to loss in functional diversity, reflected by a decrease in the number of functional traits (16). Models predict that species-poor systems have low functional redundancy and are more likely to experience functional loss with species extinction (14, 17). In comparison with many tropical terrestrial forests, mangroves are characterized by low tree species diversity (1). The continued reduction of mangrove area and cover, coupled with simplistic restoration efforts often establishing monocultures (18), is expected to result in a sharp decrease in mangrove tree biodiversity at a global scale (2). A relationship between such decline in tree diversity and the loss of mangrove ecosystem functionality has been assumed rather than demonstrated (19), as this relationship has proven difficult to measure. Significant positive correlations, however, have been demonstrated between the species richness of mangrove trees, the associated macrofauna, and potential influence on aboveground primary productivity (20). The nexus between biodiversity and

Significance

Global mangrove deforestation and degradation drive the loss of the associated invertebrate fauna vital to ecosystem services. The functional diversity and resilience of this fauna has not been assessed. We show that even small mangrove patches host functionally diverse faunal assemblages and can act as biodiversity reservoirs. However, globally, functional redundancy of mangrove invertebrates (i.e., the average number of species performing a similar functional role in an assemblage) is extremely low, except in Southeast Asia. Thus, even a modest local loss of invertebrate diversity will have significant negative consequences for mangrove functionality and resilience. Current approaches to assess threats to mangroves heavily rely on loss in areal extent, but our results suggest that loss of function may be more vulnerable.

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ecosystem functionality of species-poor systems is yet to be clarified, but a recent study of scavenging (measured by rate of fish carcasses consumed by scavengers) in Australian mangrove-fringed estuaries has highlighted the vulnerability of such systems to species loss (21).

While reliable datasets are available on global mangrove tree diversity (1, 5), no such information exists for the species composition, functional diversity, and functional redundancy of the associated fauna. The harsh environmental conditions characteristic of mangrove forests (i.e., wide daily or seasonal variability in salinity and pH, hypo-, or even anoxia of the soil) and the small number of foundation plant species compared to terrestrial forests (2) suggest a lower niche availability among mangrove resident macrofauna (22).

Mangrove ecosystems support unique faunal assemblages (22, 23), including a diverse array of sessile and mobile invertebrates, particularly crustaceans and mollusks (24, 25). Brachyuran crab assemblages are highly diverse in Indo-West Pacific (IWP) mangroves (25, 26) and are known to play a major role in ecosystem functioning (8, 20, 23). Their bioturbation activity has a significant engineering effect on the sediment through constant irrigation and oxygenation (27, 28). These crabs can also play a critical role in shaping tree dominance (29), influencing carbon cycling (30, 31), and structuring the sediment microbiome (32). The diversity of mangrove-associated gastropods also peaks in the IWP region but shows a bimodal distribution, with modes in the eastern Pacific coast of Central and South America and in Southeast Asia (33). Both gastropods and bivalves are known to be important bioengineers and bio-irrigators, playing a major role in shaping the biochemical properties of mangrove sediment and water (23).

Despite growing evidence that the functions of mangrove forests are strongly dependent on viable and diverse invertebrate assemblages (20, 23), only few studies at local scales have focused on the diversity and taxonomic structure of such assemblages. The functional richness and redundancy of the latter, critical to the ecosystems' capacity for essential services, are unknown, as are their functional vulnerability. The functional diversity of a community with species distributed in a multidimensional functional space within a given ecosystem can be quantified through indices such as functional richness [FRi—the volume of multidimensional space occupied by all species in a community within functional space (34, 35)] and functional redundancy [FRe—how redundant species and functional groups are at a given location (36)], which are increasingly used for assessing ecosystem functioning. Recently, these measures, used in parallel with functional vulnerability [FVu—the potential decrease of functional diversity as a consequence of species loss (36)], have also proven to be useful tools for assessing impacts of disturbances on ecosystems (37, 38) and for forecasting possible responses to anthropogenic perturbations (16).

In this study, we assessed the vulnerability of global mangrove ecosystems to the loss of functions mediated by macrobenthic species by computing taxonomic distinctness $\Delta+$ (39), FRi, FRe, and FVu indices based on crustacean and mollusk assemblages recorded from 16 different mangrove forests across the world. We assigned functional traits to the 209 crustacean and 155 mollusk species in our database according to their respective 1) feeding habits, 2) behavioral traits potentially affecting ecosystem characteristics, and 3) microhabitats. By using functional traits as proxies for functions, this approach allowed us to establish global patterns of macrobenthic taxonomic richness and ecosystem functionality in mangroves and to assess the vulnerability of the mangrove fauna as well as resilience of ecosystem functions mediated by them to current and future anthropogenic threats.

Results

Our sampling locations, situated in South America, Africa, the Middle East, Southeast Asia, and Australia, differ widely in terms of environmental and geographic characteristics (Table 1 and *SI Appendix*, Table S1) and level of human disturbance (*SI Appendix*, Table S2), therefore well representing the wide range of variation found among the mangrove forests of the world. Both macrobenthic taxonomic distinctness and FRi are negatively correlated with air temperature only ($F = 7.58$, $P < 0.05$, $R^2 = 0.35$ and $F = 12.43$, $P < 0.01$, $R^2 = 0.47$, marginal tests for $\Delta+$ and FRi, respectively, *SI Appendix*, Table S3). As a direct consequence, FVu is positively correlated with the same factor ($F = 5.64$, $P < 0.03$, R2 = 0.29, marginal test, *SI Appendix*, Table S3). There is a significant positive effect only of tree species richness on functional redundancy ($F = 19.71$, $P < 0.01$, $R^2 = 0.58$, *SI Appendix*, Table S3). Interestingly, the area of the forests has no effect on any of the calculated indices, with very small patches of mangroves, such as the Mozambican and the Hong Kong ones (<2.5 km^2), characterized by high taxonomic distinctness and FRi, while some large forests, such as the Cameroon location (250 km^2), depict much lower FRi (*SI Appendix*, Table S1 and Figs. 1 and 2).

As expected, taxonomic distinctness peaks at the western Pacific Ocean locations (max $\Delta+ = 80.96$) but unexpectedly also at the southern American locations ($\Delta+ > 80$), while values for both the western African and western and central Indian Ocean mangroves are intermediate ($\Delta+ > 65$), with the exceptions of Nouamghar (Mauritania, $\Delta+ < 55$) and Galle (Sri Lanka, $\Delta+ < 60$) (Table 1 and Fig. 1). FRi values show a distinct biogeographic pattern, with West African mangroves being particularly low (Fig. 2 *C* and *D*), while Indonesia and Hong Kong, our eastern Indian/western Pacific Ocean locations, display the highest values (Figs. 1 and 2 *L* and *N*). The significance of the biogeographic pattern is further highlighted by the two western African locations, both characterized by low FRi while demonstrating pronounced ecological differences, with Nouamghar (Mauritania) located in a dry region at the verge of the Sahara Desert, whereas Douala (Cameroon) has very high rainfall (Table 1). Besides the western African locations, the poorest faunas in terms of functional entities (FE) diversity were Thuwal (Saudi Arabia) and Galle (Sri Lanka), with only 16 and 17% of global FEs, respectively. These low diversity faunas, however, fill nearly the same amount of functional space as the much richer faunas recorded at the eastern African and Australian locations (Fig. 2). This stability in functional diversity is probably due to a high taxonomic similarity among faunas, at least at supraspecific level, and shows that poorer mangrove faunas share most of the key functions with richer faunas (Fig. 2).

FRe values are low at both the eastern Atlantic and the western Indian Ocean locations, where mangrove forests have less than two species per FE, the minimum value needed to provide an "insurance policy" for a particular trait (36). On the other hand, the southern American and western Pacific Ocean locations are characterized by FRe values above this critical threshold, with Segara Anakan in Indonesia having the highest redundancy (Fig. 1).

As expected, the two low-diverse arid locations of Nouamghar (Mauritania) and Thuwal (Saudi Arabia) are the most vulnerable (Fig. 1), while Moreton Bay (Australia) has the lowest value of FVu of the dataset, even though it is not the most diverse in terms of species (Fig. 1). In general, FVu values are high at the eastern and western Indian and western Pacific Ocean locations, with the notable exceptions of the two southernmost ones (Mngazana, South Africa, and Saco da Inhaca, Mozambique) and the anthropogenically impacted location of Galle (Sri Lanka) (Fig. 3*D*).

Taxonomic distinctness fits best in a logarithmic relationship with the total number of species recorded (Fig. 3*A*). It shows a rapid initial increase with total species numbers, but, when the curve reaches its asymptotic part, the values become weakly related to the total number of species present (Fig. 3*A*). Notably, Segara Anakan (Indonesia), characterized by 100 macroinvertebrate species, shows a slightly lower taxonomic distinctness in comparison to locations where <60 species were recorded, such as Bahía Málaga

Table 1. Environmental, taxonomic, and functional characterization of the sampling locations

Location	Air T (°C)	Rainfall (mm)	Mangrove Tree Species	S	FRe	FRi	FVu	Δ+
Bahía Málaga (CO)	25	7,399	5	55	2.55	0.62	0.41	82.74
Península Ajuruteua (BR)	27.7	2,500	4	48	2.40	0.43	0.55	81.77
Nouamghar (MR)	25.8	95	1	7	1.40	0.02	0.8	54.29
Douala (CM)	26.5	4,000	7	15	1.36	0.19	0.73	72.57
Mngazana (ZA)	22.8	1,000	3	21	1.40	0.45	0.67	70.57
Saco da Inhaca (KE)	22.8	1,100	4	30	1.58	0.55	0.63	70.80
Gazi	26	1,408	7	47	1.68	0.58	0.5	73.12
Mida Creek (KE)	26	1,408	7	48	1.71	0.58	0.46	73.16
Thuwal (SA)	26	56	2	12	1.20	0.32	0.8	73.64
Port Launay (SC)	27	1,600	5	20	1.54	0.16	0.62	68.00
Galle (LK)	26.5	2,380	5	17	1.55	0.18	0.73	59.41
Segara Anakan (ID)	27	3,340	21	100	3.54	0.65	0.5	79.58
Mai Po (HK)	23.3	1,600	7	50	2.04	0.72	0.5	80.73
Ting Kok (HK)	23.3	1,600	7	50	2.32	0.63	0.42	79.73
Tung Chung (HK)	23.3	1,600	7	44	2.50	0.74	0.5	80.96
Moreton Bay (AU)	22	1,600	8	26	2.00	0.54	0.31	73.66

S, number of macrobenthic crustacean/gastropod species; T, temperature; Δ+, average taxonomic distinctness. Air temperature and rainfall values are annual means.

(Colombian Pacific coast) and Península Ajuruteua (Brazilian north coast). Also, FRi shows an asymptotic relationship with the number of macrofaunal species, demonstrating that in mangrove forests, there is generally a limited number of FEs, irrespective of total faunal richness (Fig. 3*C*). In contrast, a strong relationship between the number of species and FRe is evident (Fig. 3*B*), while there is only a weak relationship between FRe and FRi (Fig. 3*E*).

Discussion

To our knowledge, our dataset is the largest and most comprehensive available on resident mangrove macrofauna to date, but it is still far from being all embracing. Insects are a large and definitely underestimated (23) component of mangroves, and they are not present in our dataset together with better-described and important populations of benthic fishes, such as mudskippers. Cryptic species such as wood borers are likely underrepresented in our dataset. Moreover, presence/absence data could mask or underestimate important trends in species dominance and differences in biomasses among locations. Notwithstanding these limitations, our collective data clearly show important patterns in the distribution of invertebrate fauna and mangrove functionality with significant implications for future biodiversity studies as well as conservation and management strategies.

Invertebrate taxonomic diversity peaks at the South American and Southeast Asian locations. We recorded relatively high values in the western Indian Ocean, besides the notable exception of Galle, Sri Lanka. The lowest value was recorded from Mauritania in the eastern Atlantic Ocean. Our analyses showed that mangrove invertebrate diversity is only marginally affected by air temperature, and it is neither influenced by tidal amplitude nor by precipitation and latitude, contrary to the drivers of mangrove plant diversity (40). Besides the Sri Lankan location, where hydrology was significantly modified, there was also little direct correspondence with the level of human intervention (*SI Appendix*, Table S2). Instead, these trends mirror the global pattern of mangrove tree diversity and support the "vicariance hypothesis" proposed for the mangrove biodiversity anomaly (1, 33). This hypothesis postulates that mangrove forests and their associated fauna evolved around the Tethys Sea, from the Late Cretaceous through the Early Tertiary, and that their present distribution is the result of differential extinctions and local vicariance events.

Taxonomic distinctness was correlated to total species numbers, with similar Δ+ values for locations and recorded species numbers ranging from 48 to 100. This shows that this index, based on phylogenetic relationships among species, is a powerful tool to infer the taxonomic composition of mangrove macrofaunal assemblages. The asymptotic relationship evidences that, irrespective of the total number of species of crustaceans and mollusks found in a mangrove forest, most belong to a small number of highly specialized families, which are clearly the only taxa capable of adapting to these harsh environments. Throughout the extant mangrove range, the brachyuran families Sesarmidae, Ocypodidae, and Macrophthalmidae as well as gastropods belonging to Littorinidae, Potamididae, and Ellobiidae are consistently the most widespread, abundant, and dominant taxa. Although present in other habitats, these taxa show the highest degrees of adaptation, such as arboreality and leaf litter feeding behavior (23).

The FRi of invertebrate assemblages proved to be a powerful tool to identify both the biogeographic trends of functionality and impact of anthropogenic changes to local hydrology. Similar to taxonomic distinctness, there was only a significant negative relationship between this index and temperature, showing that, within most of their geographic range, mangrove forests host functional invertebrate assemblages under a broad range of environmental conditions. Indeed, significant differences in functional richness mirroring the global biogeographic patterns of mangrove tree diversity were detected, with West African mangroves being particularly poor, while Indonesia and Hong Kong, in the eastern Indian and western Pacific Ocean, displaying the highest values. Two notable cases of low functional richness were represented by Nouamghar in Mauritania and Galle in Sri Lanka. In the former case, both biogeographic and harsh environmental factors result in low tree diversity, leading to a limited number of taxa and functional traits represented in the faunal community. This northernmost distribution of mangroves at the verge of the Sahara Desert only hosts 40% and 50% of the feeding and bioengineering traits, respectively, considered in the present study. However, the low functional richness of Galle cannot be explained by biogeography or environmental harshness. Due to anthropogenic changes to the hydrology (*SI Appendix*, Table S2), much of the forest floor at this location is constantly submerged (41). The altered tidal regime excludes most of the microphytobenthos feeders common in the Indo-Pacific mangroves, such as Macrophthalmidae and sand bubbler crabs (Dotillidae), and also alters the distribution of fiddler crabs (Ocypodidae), which feed on more frequently immersed substrates. The absence of burrowing and feeding activities performed by the above families of crabs reduces bioturbation, likely resulting in significant shifts in biogeochemistry,

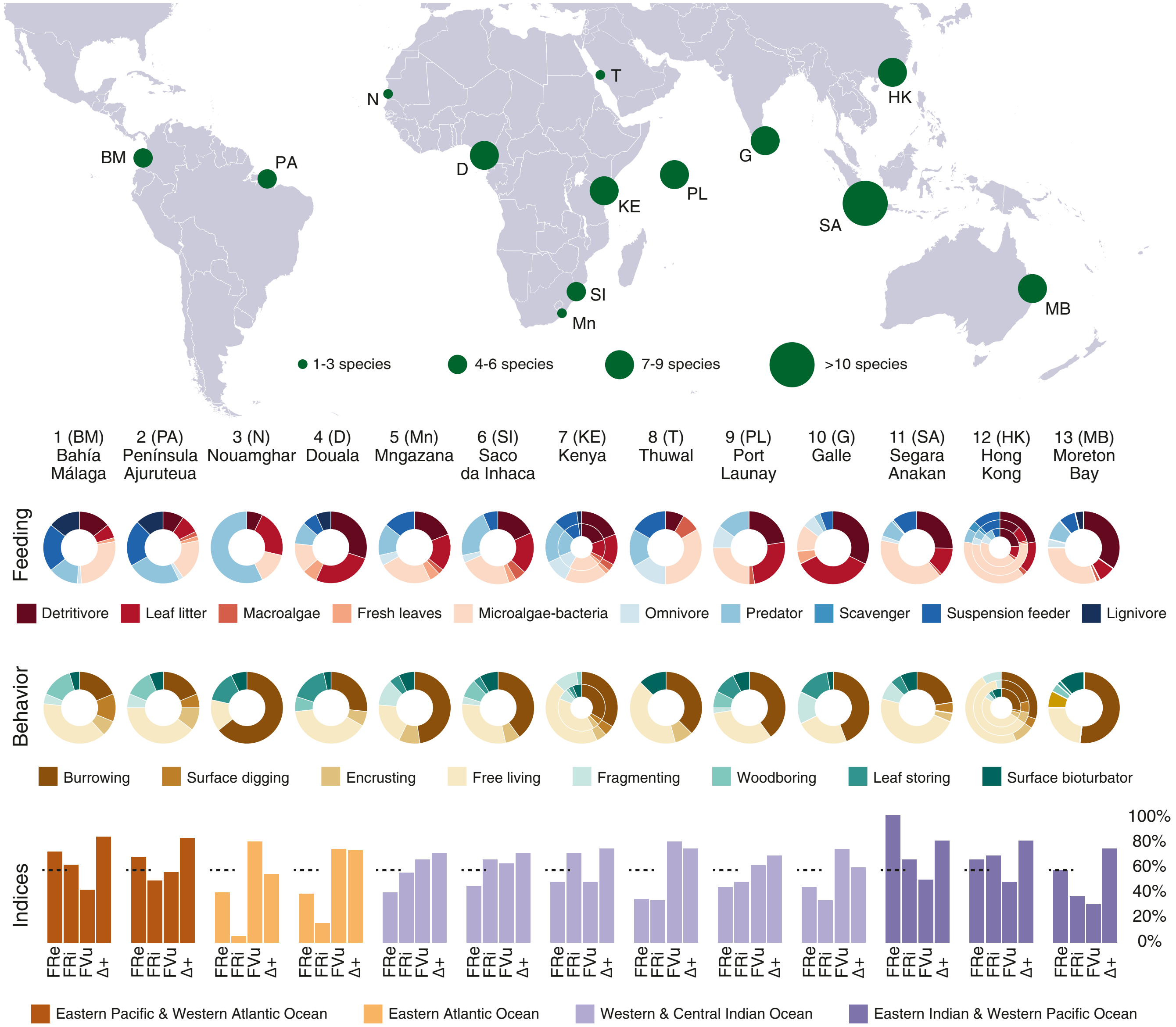

Fig. 1. Representation of the 16 sampling locations across the globe with their macrofaunal descriptors (data for crustaceans and mollusks pooled) and range of mangrove tree species richness. The tree species richness at each sampling study location is indicated in Table 1. The two rows of doughnut charts show the different functional traits and proportion of the crustacean and mollusk species with such traits per location. Embedded doughnut charts are shown for countries with multiple sampling locations. (*Bottom*) The four calculated indices expressed as percentage for standardization, with FRe on the left, FRi and FVu in the middle, and taxonomic distinctness (Δ+) on the right. The dashed lines above FRe represent the minimum value of species necessary (two species) to ensure redundancy of functionality.

for example, nutrient fluxes, and redistribution in the surface sediment (27) and bacterial communities (32), with strong implications for ecosystem dynamics (41).

FRe reflects the average number of species with the same combination of functional traits found in an assemblage. A reliable proxy to ensure redundancy is an overall minimum of FRe = 2 (36). This index was below that threshold in >60% of the studied locations, with the notable exceptions being locations in South America and the eastern Indian and western Pacific Ocean. The biogeographic patterns of invertebrate functional redundancy mirrored the global anomaly of mangrove tree species richness. This relationship may be explained by the fact that an increased mangrove tree diversity provides a wider array of microniches, resulting in a redundancy of species performing similar roles in adjacent microhabitats within the forests. FRe is also a powerful tool to assess ecosystem degradation and can help identify the faunal species most vulnerable to local extinction (37). These species usually possess unique trait combinations that, if lost, could result in the disappearance of significant ecosystem roles (42). Our analyses show that within mangrove forests, on average, 57% of the total functional trait combinations have little "insurance" and are performed by a single species, confirming that even a small loss of diversity could have significant negative consequences for the ecosystem (*SI Appendix*, Fig. S1). An overall comparison between our results and the ones obtained using the same indices for other ecosystems reveals that mangrove forests are ecosystems with one of the lowest faunal FRe recorded to date (Table 2).

Lastly, FVu clearly demonstrates the ecological fragility of mangroves thriving in extreme environments, such as the arid Sahara and Arabic coasts or at the southernmost limits of mangrove distribution in Africa (*SI Appendix*, Fig. S1). Extreme high

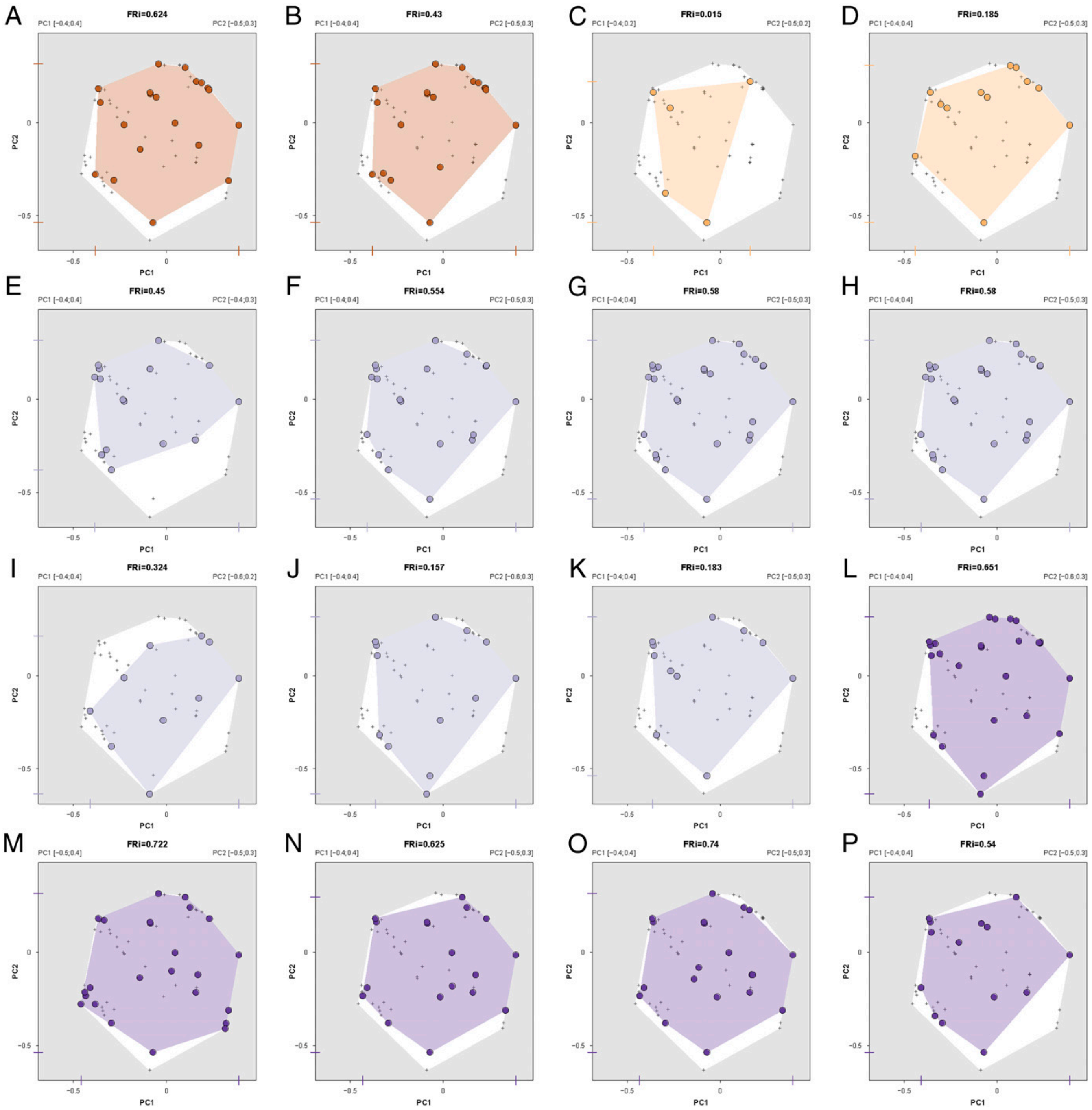

Fig. 2. Principal component analysis graphs representing the FRi (colored area) at the different study locations in relation to the overall functional space (white area) occupied by the total amount of species identified in this study. Species that are present in a specific location are highlighted with colored dots, while the remainder of the species present in the dataset of the entire study are represented with crosses. The locations are in the same order as in Fig. 1: (*A*) Bahía Málaga (Colombia); (*B*) Península Ajuruteua (Brazil); (*C*) Nouamghar (Mauritania); (*D*) Douala (Cameroon); (*E*) Mngazana (South Africa); (*F*) Saco da Inhaca (Mozambique); (*G*) Gazi (Kenya 1); (*H*) Mida Creek (Kenya 2); (*I*) Thuwal (Saudi Arabia); (*J*) Port Lunay (Seychelles); (*K*) Galle (Sri Lanka); (*L*) Segara Anakan (Indonesia); (*M*) Mai Po (Hong Kong 1); (*N*) Ting Kok (Hong Kong 2); (*O*) Tung Chung (Hong Kong 3); and (*P*) western Moreton Bay (Australia). The different colors of the space representing the FRi relates to the region of the study locations (see Fig. 1 for color key).

levels of functional vulnerability, suggesting a potentially rapid decrease of functional diversity, were also found in Galle (Sri Lanka), where an irreversible change in hydrology is known to have caused a cryptic ecological degradation of the forest (13).

The combination of the complementary information provided by the indices of taxonomic distinctness, FRi, FRe, and FVu is key to the understanding of the ecological state of a mangrove forest, to evaluate its resilience to environmental change, and to design ecologically sound conservation and restoration plans. Good examples are the East African locations where relatively high values of both taxonomic distinctness and FRi seem to suggest at first glance that these forests are in a good state. Compared to other geographic areas, these systems have suffered low rates of destruction (2, 5) and still host a functionally

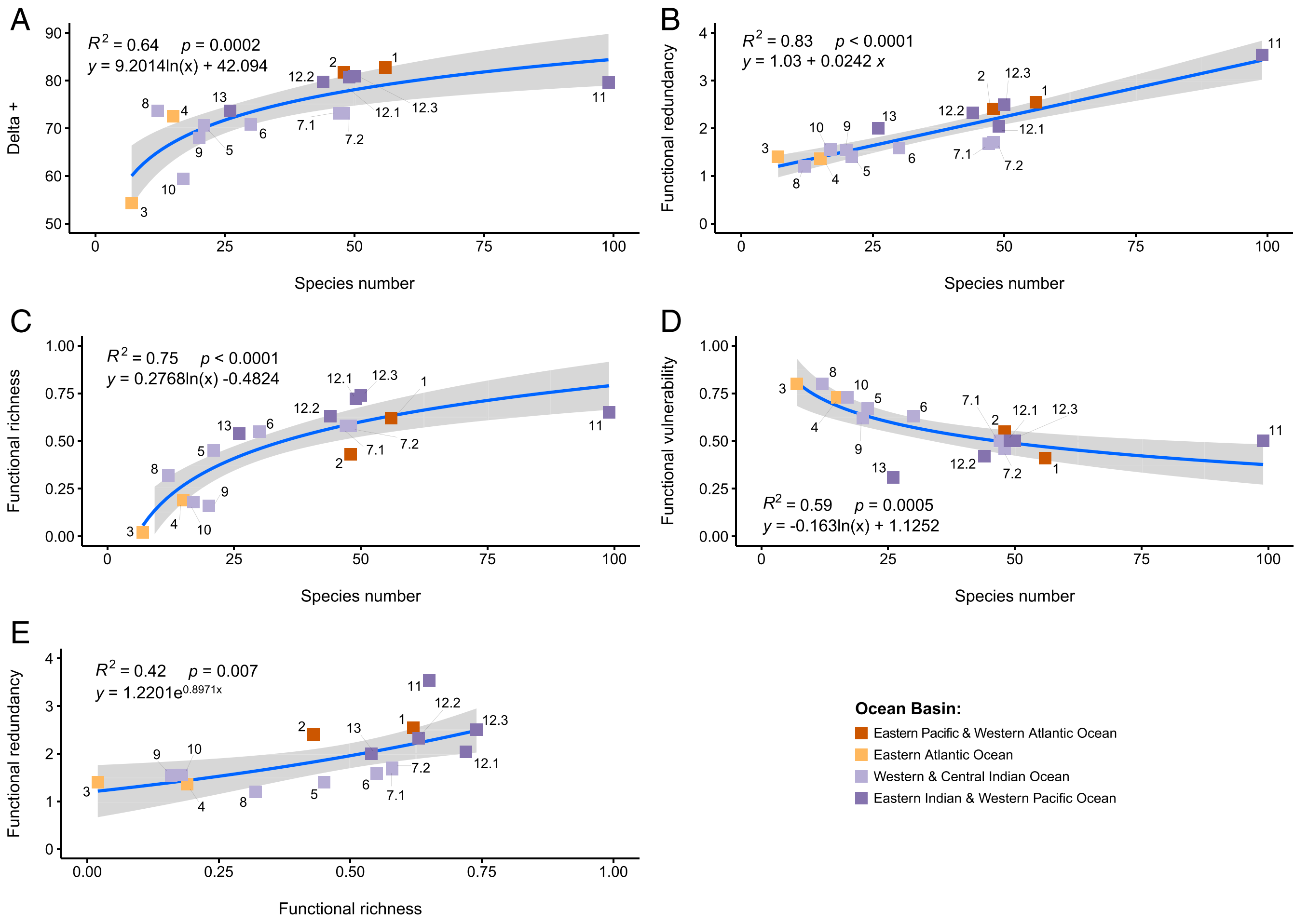

Fig. 3. Relationships among number of macrobenthic species recorded (see Fig. 1 for key to locations) and the computed taxonomic and functional indices. Best fitted trend lines (dotted blue line) and the associated R^2 value are shown for (*A*) taxonomic distinctness (Δ+) and species number with a logarithmic trend line; (*B*) FRe and species number with a linear trendline; (*C*) FRi and species number with a logarithmic trend line; (*D*) FVu and species richness with logarithmic trend line; and (*E*) FRe and FRi with an exponential trend line.

rich invertebrate fauna. However, given their critically low FRe values, their resilience, that is, capacity for resisting future changes, is likely low (*SI Appendix*, Fig. S1).

Another striking finding of our integrated approach is that none of the measured indices was related to the size of the studied forest. We have shown how even small mangrove patches, such as those in Hong Kong and Mozambique, harbor highly diverse and functionally rich invertebrate assemblages. Small forests can therefore still be functional and represent true biodiversity reservoirs, harboring source populations of highly diverse invertebrate assemblages, which could prove critical to the recruitment and restoration of the fauna of connected proximal or distant habitat patches. While the conservation of extensive, pristine, and diverse mangrove forests should be prioritized (19), our results show that the preservation of small yet well-connected patches of mangroves is also important (43).

Conventional attention on threats to mangrove ecosystems focuses heavily on their areal extent (3, 4, 6). Our results, however, suggest that their functional integrity may be even more vulnerable toward environmental change since many critical functions and

Table 2. Low functional redundancy values of mangrove macrobenthic assemblages

			FRe following (36) $FRe = \frac{S}{FE}$							
			Benthic marine biota (56)			Reef fishes (17)	Reef fishes (36)			Freshwater fishes (59)
	Mangrove invertebrate fauna (this study)	Corals (55)	Cambrian	Silurian	Modern			Reef fishes (57)	Lichens (58)	
Min	1.2	1.7	NA	NA	2.5	5	2.5	2.3	4.5	1.6
Max	3.5	2.8	NA	NA	7.9	6	7.9	3.3	6.3	2.6
Mean	1.9	2.2	2.1	2.5	5	5.4	5	2.7	5.4	2.2
SD	0.6	0.5			2.1	0.5	2.1	0.2		0.2

The table shows comparisons among the values of FRe computed in the present study and the ones found for other ecosystems, calculated using the same method. NA = not available.

services that mangrove forests provide are supported by the synergistic interactions of their floral and faunal components (8). Here, we advocate that for the evaluation of ecosystem status, functionality, and resilience of mangrove forests, it is crucial to study the composition and traits of the resident faunal assemblages. In this study, we have based our assessment of ecosystem vulnerability on FRe. As mangroves are spatially diverse and temporally dynamic, long-term monitoring programs will be necessary to establish the redundancy–vulnerability relationship in these systems. The intrinsically low taxonomic diversity and FRe of their resident fauna suggest that mangrove forests are some of the most vulnerable ecosystems on the planet, except for the speciose systems in Southeast Asia. Forests in this region, however, are among the most threatened in the world due to extensive conversion into aquaculture ponds or oil palm plantations (3). A holistic approach, based on ecological characteristics and combining information on both floral and faunal functionality, must underpin effective future management, conservation, and restoration strategies for these threatened ecosystems (18) to ensure the sustained provision of their critically important services.

Materials and Methods

Dataset. To ensure a reliable presence/absence information of mangrove crustaceans and mollusks for our analyses, only data collected at the own research locations of the coauthors, all with taxonomic expertise in mangrove fauna in different parts of the world, were used. Numerous surveys were performed within the period 1985 to 2020 involving various standard techniques, ranging from manual collection, visual observation, and trapping due to the complexity of the mangrove habitat and the different behaviors of the macrobenthic species (*SI Appendix*, Table S5). Some of the individual datasets (or parts thereof) are published, such as the Colombian (44), Brazilian (45, 46), Indonesian (25, 47), Gazi [Kenya (24)], Saco da Inhaca [Mozambique (24)], and Douala (48) studies. The sites varied in degree of human intervention from locally absent (Nouamghar, Mauritania) to high (e.g., Indonesia) (*SI Appendix*, Table S5).

Indices and Metrics. As a measure of faunal diversity, we used the average taxonomic distinctness index (Δ+), which summarizes the overall hierarchical structure of an assemblage (49). This index is also robust for big sets of data collected using several techniques, as in our case, and different sampling efforts (39). For the functional analyses, three categorical traits only were used to assess the different functional indices to avoid both redundancy in the traits chosen and an overrepresentation of their role in the ecosystem (50) (*SI Appendix*, Table S4). We could then identify 64 FEs based on unique combinations of the abovementioned categorical functional traits to classify the 364 species of resident mangrove invertebrates identified at our locations. We also built a functional space where FEs were placed according to their trait combinations (Fig. 2) (36). The three traits chosen were the following: 1) feeding habits, 2) behavioral traits potentially affecting ecosystem characteristics, and 3) microhabitat position (*SI Appendix*, Table S4). The position of the animals sampled inside the mangrove forests was coded using four categories: supratidal, intertidal forest, intertidal mudflat, and subtidal.

Dietary categories were coded using a fuzzy logic approach in which different diets were assigned to the present species, allowing a species to feed on more than one item. A total of 10 dietary categories were considered, namely the following: detritivore, leaf litter and propagule feeder, macroalgal feeder, fresh mangrove leaf feeder, microalgae and bacteria feeder, omnivore, predator, scavenger, suspension feeder, and lignivore (Fig. 1 and *SI Appendix*, Table S4). To further assess the ecological impact of the various species, eight behavioral categories were identified, also using a fuzzy logic approach: burrowing, surface digging, encrusting, free living, shredding, wood boring, leaf storing, and surface bioturbating (Fig.1 and *SI Appendix*, Table S4). All encountered crustacean and mollusk species were then assigned to the different categories according to expert knowledge of the authors and the available literature. A detailed description of the above traits and categories is provided in *SI Appendix* and in *SI Appendix*, Table S4.

The separation among functional traits was computed using Gower distance, allocating the same weight to all three traits. Principal coordinate analysis was conducted using this matrix, and the coordinates were then used to construct a multidimensional space with four axes to allow for the calculation of FRi (Fig. 2). FRi was assessed by measuring the proportional convex hull volume of the multidimensional space occupied by all species in a community within the functional space (37). A higher FRi indicates that the community has a large representation of trait combinations present, while a lower one denotes that only a few traits are present in the community. FE represents a unique combination of traits present at a given location (36), with its number varying from five to 28 across the different study locations. FRe and FVu were calculated following the method suggested by Mouillot and coworkers (37),

$$\mathrm{FRe} = \frac{\sum_{i=1}^{\mathrm{FE}} n_i}{\mathrm{FE}} = \frac{S}{FE}$$

$$\mathrm{FVu} = \frac{\sum_{i=1}^{\mathrm{FE}} \min(n_i = 1)}{\mathrm{FE}},$$

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

Linear models were built to determine which environmental and geomorphic variables best explained the variability of the four computed indices across locations. For each index, the best possible combination of predictor variables was selected through a stepwise procedure and using a modification of the Akaike Information Criterion developed to cope with datasets with a low number of samples with respect to the number of predictor variables (the AICc criterion). All the applied stepwise procedures began with a null model to which a predictor variable was added to improve the AICc criterion. (*SI Appendix*, Table S3). Univariate marginal tests were also performed for each predictor variable. All indices were computed and analyses performed in PRIMER 7 software and R (51). The packages *ade4* (52) and *vegan* (53) in R, in addition to R scripts provided by refs. 36 and 37, were also used.

Data Availability. Species occurrence data together with location metadata have been deposited in the University of Hong Kong (HKU) DataHub and DataCite (10.25442/hku.12830951.v1) (54).

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Supporting Information for

A functional approach reveals extremely low redundancy in global invertebrate mangrove fauna

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Description and categorization of functional traits for mangrove invertebrate macrofauna

Mangrove ecosystems support specialized resident invertebrate assemblages, mainly dominated by crustaceans (particularly brachyuran crabs) and mollusks (mostly gastropods) (1, 2). It is becoming evident that healthy and resilient mangrove forests support diverse invertebrate assemblages (3–5). The ecological role of each species depends on its biological and behavioral traits, which has never been identified and categorized in an integrated approach for resident mangrove fauna. For instance, the burrowing and feeding activity of some crab species have an ecoengineering effect on mangrove forests (6–8), while the litter storing and consumption behavior of other species affects carbon fluxes and nutrient retention (9). Many gastropods also mediate nutrient fluxes by feeding on mangrove litter as well as the microphytobenthos (2). For the above reasons, we identified and categorized three traits related to the major ecological roles exerted by the invertebrate fauna on mangrove ecosystems.

Position along the intertidal belt. Mangrove resident fauna is known to be spatially segregated along the sea-land axis, in a distribution typical of intertidal habitats (10–12). The intertidal position occupied by a species determines its ecological impact on prey populations (including food plant species), making tidal position a crucial trait to characterize the species' niche (Table S2).

Diet. Diet determines the position of a species within the mangrove food web and its trophic role (3, 13, 14). In particular, diet is strongly correlated with the feeding and foraging behavior, as well as the morphology of many mangrove invertebrates, which typically rely on two primary sources of carbon and nitrogen. Most of the sesarmid crabs and one ocypodid, *Ucides cordatus*, as well as a few gastropods, such as *Terebralia palustris,* rely on mangrove litter and propagules (2, 5, 15, 16), while other ocypodids, dotillids and the majority of gastropods feed on the microphytobenthos present on the sediment surface (Table S4) (2, 17–19).

Behavior. Behavioral patterns of resident invertebrates have paramount importance for the functioning of mangrove ecosystems, ultimately affecting their capacity for service provision (2, 3, 20, 21). Burrowing activities, for instance, modulate nutrient and gas fluxes in the sediment (7, 22–26), shredding of fresh leaves and litter accelerate their decomposition (27, 28), while suspension feeders greatly improve water quality (Table S4). In particular, we used the following categories: burrowing, - species that dig and maintain their own burrows; surface digging - species that dig superficial and temporary refuges; encrusting - species encrusting mangrove trunks and roots; free living - mobile species that do not actively dig their own refuges; fragmenting - species that shred and fragment leaves and propagules while consuming them; woodboring - species that excavate their refuges inside mangrove trunks and roots; leaf storing,- species that actively store mangrove leaves and propagules in their burrows; surface bioturbating - species that actively scoop the surface sediment to feed.

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Figures and Tables

Figure S1. Modelled scenarios of species extinction at the sampled sites in relation to the observed number of Functional Entities. To estimate the speed of decline in functionality for each site, a random species was removed from the community alongside its corresponding functional entities. The process was repeated for 1000 iterations until there were no more functional entities and all species in the population were extinct. The data points are plotted with confidence intervals which are represented with horizontal dashes. The sites are in the same order as in Figure 1: A) Báhia Málaga (Colombia); B) Península Ajuruteua (Brazil); C) Mamgar (Mauritania); D) Douala (Cameroon); E) Mngazana (South Africa); F) Saco da Inhaca (Mozambique); G) Gazi (Kenya 1); H) Mida Creek (Kenya 2); I) Thuwal (Saudi Arabia); J) Port Launay (Seychelles); K) Port Galle (Sri Lanka); L) Segara Anakan (Indonesia); M) Mai Po (Hong Kong 1); N) Ting Kok (Hong Kong 2); O) Tung Chung (Hong Kong 3); and P) Moreton Bay (Australia). The different colors of the models relate to the region of the study locations (see Fig 1 for color key).

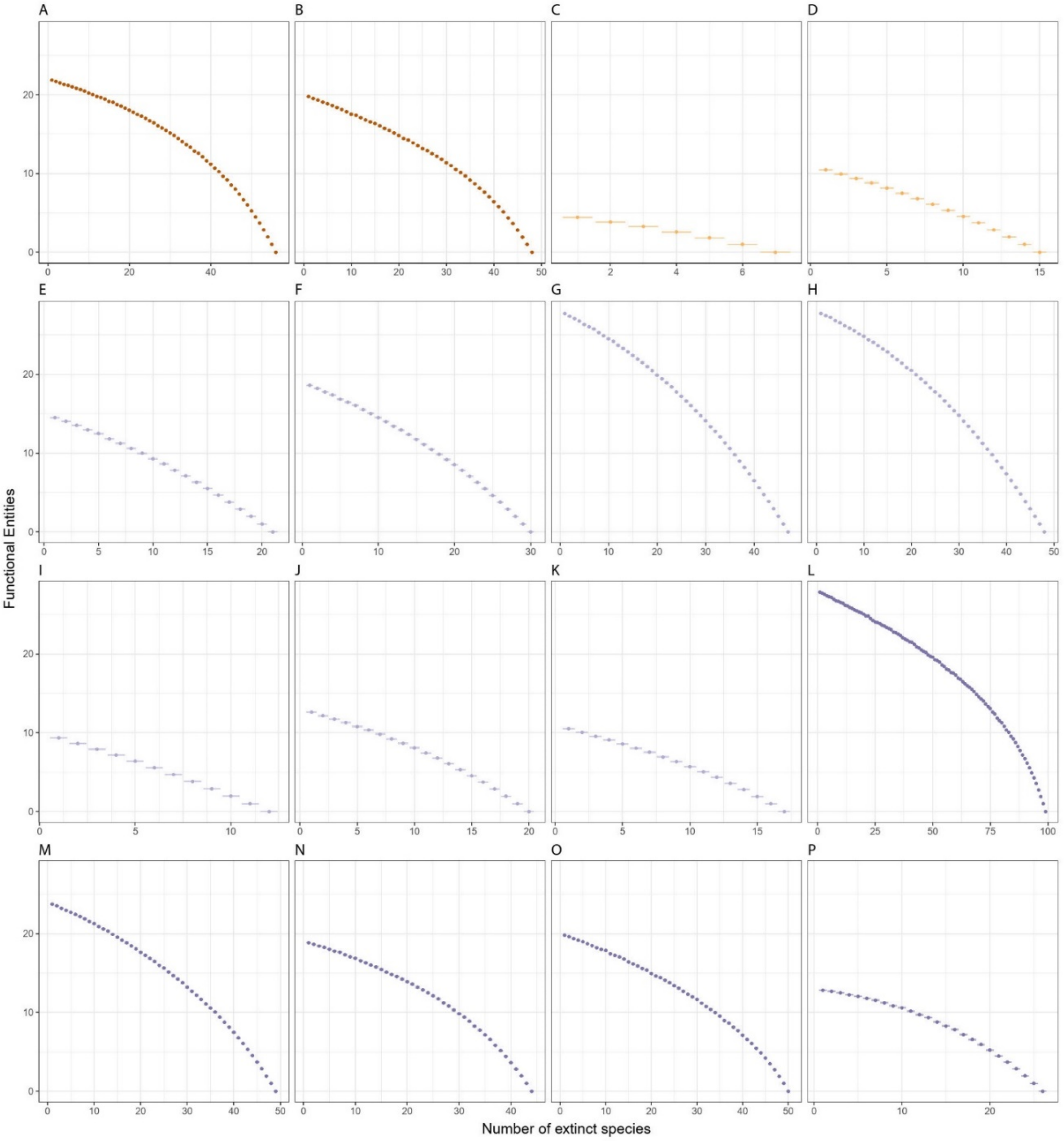

Table S1. Environmental characteristics of the sampling locations. Abbreviations as follows: Long / Lat = Longitude / Latitude; AGB = Above-ground biomass.

Country	Location	Long (°)	Lat (°)	Area (km^2)	Tidal Regime	Tree AGB (Mg.ha^{-1})
Colombia	Bahía Málaga	-77.31	3.97	44	Macro	253.2
Brazil	Península Ajuruteua	-46.68	-0.89	160	Macro	158.7
Mauritania	Nouamghar	-16.07	17.40	0.1	Meso	100.0
Cameroon	Douala	9.76	4.14	250	Macro	250.0
South Africa	Mngazana	29.39	31.69	12	Meso	80.0
Mozambique	Saco da Inhaca	32.54	26.20	2.1	Meso	100.0
Kenya	Gazi	39.31	-4.25	10	Meso	180.0
Kenya	Mida Creek	39.98	-3.35	16.6	Meso	180.0
Saudi Arabia	Thuwal	39.50	22.16	5	Meso	133.6
Seychelles	Port Launay	55.47	-4.70	1.3	Meso	136.4
Sri-Lanka	Galle	80.25	6.03	0.2	Micro	230.9
Indonesia	Segara Anakan	108.89	-7.71	92	Meso	101.7
Hong Kong	Mai Po	114.05	22.50	1	Meso	140.0
Hong Kong	Ting Kok	114.12	22.28	0.1	Meso	140.0
Hong Kong	Tung Chung	113.93	22.28	0.02	Meso	140.0
Australia	Moreton Bay	153.25	-27.25	150	Meso	135.2

Table S2. Anthropogenic interventions at the study sites. 1: Present, 0: Absent, n/a: not applicable. Resource extraction: S - for own use, IS – for income generation realized by individuals and/or for small local companies; IL – for income generation realized by large companies (locally based or beyond). Superscripts refer to complementary information underneath the table. Entries relate to the period sampled.

Country	**Location**	**Protected Area Status**	**Resource Extraction**				**Road within 1 km**	**Town/City ≥ 5000 inhabitants within 20 km**	**Agriculture / Pastoralism within 5 km**	**Commercial Aquaculture within 5 km**	**Dams or Dykes within catchment**	**Industrial Structures within 5 km**
			Brachyura	**Mollusca**	**Timber**	**Firewood**						
Colombia	Bahia Málaga[1]	National Natural Park (IUCN II)	S, IS	S, IS	S	Unknown	0	0	1	0	0	0
Brazil	Peninsula Ajuruteua[2]	Extractive Reserve (IUCN IV)	S, IS	S, IS	S, IS	S, IS	1	1	1	0	0	0
Mauritania	Nouamghar[3]	Banc d'Arguin National Park IUCN II	0	0	0	0	0	0	0	0	0	0
Cameroon	Douala[4]	0	S, IS, IL	S, IS, IL	S, IS, IL	S, IS, IL	1	1	0	0	0	1
South Africa	Mngazana[5]	0	S, IS	0	S, IS	S, IS	1	1	1	0	n/a	0
Mozambique	Saco da Inhaca[6]	Reserva da Inhaca	S, IS	S	S	0	0	0	1	0	n/a	0
Kenya	Gazi[7.1]	National Protection	S	S	S	S, IS	1	1	1	0	0	0
Kenya	Mida Creek[7.2]	National Protection and Watamu National Marine Reserve	S, IS	0	S, IS	S	1	0	1	0	n/a	0
Saudi Arabia	Thuwal[8]	Local Natural Protected Area	0	0	0	0	1	1	0	0	n/a	0
Seychelles	Port Launay[9]	Ramsar Site	S	S	S	Unknown	1	1	0	0	n/a	0
Sri Lanka	Galle[10]	0	S, IS	S, IS	S	S	1	1	1	0	1	1
Indonesia	Segara Anakan[11]	0	S, IS	S	S, IS	S	1	1	1	1	1	1
Hong Kong	Mai Po[12.1]	WWF Nature Reserve	0	0	0	0	1	1	0	1	0	1
Hong Kong	Ting Kok[12.2]	0	S	S	0	0	1	1	0	0	1	1
Hong Kong	Tung Chung[12.3]	0	S	S	0	0	1	1	0	0	0	1
Australia	Moreton Bay[13]	Marine Park	S	S	0	0	1	1	0	0	0	1

[1] Overall low degree of human intervention; estuarine mangrove on the pacific coast reachable by boat or plane only; next city (> 5000 inhabitants) and industry 37 km by boat. Two villages nearby totalling 3000 inhabitants and several small villages < 500 people. Resource exploitation only permitted for locals.

[2] Low to intermediate degree of human intervention; peninsular Amazonian estuarine mangrove part of the world's second largest continuous mangrove belt. Four adjacent villages (4700 inhabitants in total) and nearby city with 65,000 inhabitants (Bragança); Protected Extractive Reserve status since 2005, co-managed with significant legal fishery of the mangrove crab *Ucides cordatus*; some illegal timber extraction; degraded area in the mangrove from road construction in the 70s from road construction. Over 40 guesthouses/restaurants at nearby beach, increased fishing activities in holiday periods.
[3] Lack of local human interventions; northernmost mangrove in Africa fringing the shores of Sahara Desert. Very dry all year round, no rivers. Very small fishing village nearby.
[4] High degree of human intervention; estuarine mangrove bordered by Duala City with > 2 millions of inhabitants and large commercial harbour (key trading hub in W-Africa); large oil-refinery and chemical factories.
[5] Intermediate degree of human intervention; southernmost mangrove in Africa and third largest (estuarine) mangrove in South Africa; no protection status despite advocacy for its conservation; 18 to 50% of mangrove area affected by timber extraction; browsing by cattle and human trampling of seedlings; some localised sand mining for road construction.
[6] Overall low degree of human intervention; fringing mangrove located on an island reserve, low human population density. The only human impact on the island are two tourist resorts. Very small artisanal fishery to supply the tourist resorts.
[7.1] Intermediate degree of human intervention; fringing mangrove in southern Kenya, with some smaller rivers. All Kenyan mangroves are protected by national law, but no enforcement. Small villages are bordering and impacting the forest with sewage; very small-scale crab and mollusc fishery.
[7.2] Intermediate degree of human intervention; fringing mangrove in northern Kenya, with some smaller rivers. All Kenyan mangroves are protected by national law, but no enforcement. Small villages are bordering and impacting the forest with sewage; very small-scale crab and mollusc fishery.
[8] Intermediate degree of human intervention; fringing mangrove bordered by Thuwal city (7600 inhabitants), the Campus of King Abdullah University of Science and Technology (approx. 5000 people) and desert. Area under increasing development.
[9] Overall low degree of human intervention and one of the best-remaining (fringing) mangrove forest on Mahe Island. The entire bay is a no-fishing area, access for tourism purposes in permitted, touristic estates present around the area.
[10] High degree of human intervention, estuarine mangrove forest exposed to a variety of anthropogenic impacts ranging from sewage, concrete production industry to damming and resource extraction. Data were collected prior to the designation of the protected-area status.
[11] High level of human intervention; Mangrove-fringed lagoon, adjacent rural settlements, rice fields, aquaculture, industrial areas (including largest oil refinery of Indonesia); Cilacap city at the coast with 201,000 inhabitants.
[12.1] High degree of human intervention; located in the Pearl River Estuary inhabited by > 30 million people. Largest mangrove site in Hong Kong territory, expanding naturally. Located in front of the large Shenzen harbor. Diverse industrial structures and industrial hotspot of China.
[12.2] Intermediate degree of human intervention; fringing mangrove located in a relatively rural area of the Hong Kong territory, but close to the Industrial Estate of Tai Po. It is located within the Tolo Harbour complex, which is strongly polluted in terms of nitrogen, regular events of hypoxia..
[12.3] High degree of human intervention; estuarine mangrove located on Lantau Island, right in front of Hong Kong International Airport and bordered by a town with 125,000 inhabitants.
[13] Low to intermediate degree of human intervention of fringing mangroves located close to a city of >1.5 million people. Part of a large marine park divided into various levels of use, with strictly enforced management of the area. Some significant infrastructure, including an international airport, a sewage treatment facility and an oil refinery are present. Industries are supposed to strictly observe environmental rules on discharge, emissions etc.

Table S3. Linear models built to test which environmental and geomorphic variables explained at best the variability of taxonomic distinctness, functional richness, functional redundancy and functional vulnerability. For each index, the variables selected by the step-wise procedure are shown together with the treatment sum of squares (Trat. SS), the values of the F-statistics and P, the proportion of variability explained by the single variable (prop.) and by the various variables added to the model (Cumul.), the residual degrees of freedom (Res. Df) and the Akaike information criterion with a correction for small samples (AICc). For each index, the best overall linear model capable to explain its variability is also shown together with the predictor variables involved, the residual sum of squares (Res. SS), R^2 and AICc.

Taxonomic distinctness	Variables in the model	Treat. SS	F	P	Prop.	Cumul.	Res. df	AICc
	+Air T	334.450	7.579	0.027	0.351	0.351	14	63.380
	+ Tide	177.300	5.233	0.046	0.186	0.537	13	61.044
	+ Tree AGB	175.600	7.956	0.016	0.184	0.722	12	56.543
	+ Latitude	72.089	4.114	0.071	0.076	0.798	11	55.823
	Overall Best result for the linear models	Res. SS	R^2	AICc				
	Latitude, Air T, Tree AGB, Tide	192.78	0.798	55.823				
Functional richness	Variables in the model	Treat. SS	F	P	Prop.	Cumul.	Res. df	AICc
	+ Air T	0.349	12.403	0.002	0.470	0.470	14	-54.354
	+ Mangrove tree species	0.086	3.650	0.055	0.116	0.586	13	-55.236
	Overall Best result for the linear models	Res. SS	R^2	AICc				
	Air T, Mangrove tree species	0.307	0.586	-55.236				
Functional redundancy	Variables in the model	Treat. SS	F	P	Prop.	Cumul.	Res. df	AICc
	+ Mangrove tree species	3.298	19.708	0.003	0.585	0.585	14	-25.819
	+ rainfall	0.417	2.817	0.120	0.074	0.659	13	-25.881
	+ Tree AGB	0.451	3.674	0.083	0.080	0.739	12	-26.518
	+ Latitude	0.498	5.615	0.036	0.088	0.827	11	-28.753
	Overall Best result for the linear models	Res. SS	R^2	AICc				
	Mangrove tree species, rainfall, Tree AGB, Latitude	0.976	0.827	-28.753				
Functional vulnerability	Variables in the model	Treat. SS	F	P	Prop.	Cumul.	Res. df	AICc
	+ Air T	0.092	5.643	0.023	0.287	0.287	14	-63.043
	Overall best result for the linear models	Res. SS	R^2	AICc				
	Air T	0.229	0.287	-63.043				

Table S4. Traits and categories used to identify the functional entities (FEs) utilized in the analyses. For each category, some example species are shown (full species list available from https://doi.org/10.25442/hku.12830951.v1), together with the relevant references.

Trait	Category	Example species	Reference
Spatial position	supratidal	*Cardisoma guanhumi, Orisarma intermedium*	(29, 30)
	intertidal forest	*Ucides cordatus, Parasesarma guttatum, Terebralia palustris*	(31–33)
	intertidal mudflat	*Metaplax elegans, Gelasimus* spp., *Pirenella* spp.	(30, 34, 35)
	subtidal	*Thalamita crenata, Scylla* spp.	(36, 37)
Diet	detritivore	*Chasmagnathus convexus, Merguia oligodon*	(38, 39)
	leaf litter and propagule feeder	*Ucides* sp., *Neosarmatium* spp., *Terebralia palustris*	(11, 31, 40–42)
	macroalgal feeder	*Metopograpsus* spp.	(43–45)
	fresh mangrove leaf feeder	*Leptarma leptosoma, Aratus* spp.,	(46–48)
	microalgae and bacteria feeder	*Leptuca* spp., *Gelasimus* spp., *Austruca* spp., *Cerithidea* spp.	(19, 35, 49)
	omnivore	*Selatium elongatum, Clibanarius* spp., *Alpheus colombiensis*	(17, 44, 50, 51)
	predator	*Epixanthus dentatus, Scylla* spp.	(52, 53)
	scavenger	*Nassarius* spp.	(54)
	suspension feeder	*Petrolisthes armatus, Saccostrea cucullata, Isognomon ephippium*	(55, 56)
	lignivore	*Neoteredo reyni*	(57)
Behavior	burrowing	*Ucides cordatus, Neosarmatium* spp., *Austruca* spp.	(58–61)
	surface digging	*Geloina* spp.	(62)
	encrusting	*Saccostrea cucullata, Isognomon ephippium*	(55, 56)
	free living	*Metopograpsus* spp., *Aratus* spp.	(43, 63)
	fragmenting	*Parasesarma bidens, Parasesarma affine*	(64, 65)
	woodboring	*Neoteredo reyni, Barnea subtruncata*	(57)
	leaf storing	*Neosarmatium* spp.	(9, 11, 42, 66)
	surface bioturbating	*Leptuca* spp., *Gelasimus* spp., *Austruca* spp.	(19, 49, 60, 67)

Table S5. Details on sampling regime. Sampling methods: 1 – Macrobenthos collection on sediment (including among litter), roots, lower trunks and branches; 2 – Digging and/or sediment sieving; 3 – Binocular observations; 4 – Trapping (pitfall traps).

Country/Region	Location	Year	Period	Sampling methods	Example reference
Colombia	Bahia Málaga	1985-88, continued to 2018	Day	1, 2, 3	(68)
Brazil	Peninsula Ajuruteua	1996-2003, continued to 2014	Day	1, 2, 3	(49, 69, 70)
Mauritania	Nouamghar	1998-2009	Day & night	1, 2, 3	
Cameroon	Douala	2009	Day	1, 3	(71)
South Africa	Mngazana	1999-2018	Day & night	1, 3	(72,73)
Mozambique	Saco da Inhaca	2009	Day & night	1, 2, 3	(72, 74, 75)
Kenya	Gazi	1998-2009	Day & night	1, 2, 3	(74,75)
Kenya	Mida Creek	1998-2008	Day & night	1, 2, 3	(72, 76)
Saudi Arabia	Thuwal	2014-2019	Day & night	1, 2, 3	(76)
Seychelles	Port Lunay	2005	Day & night	1, 3	
Sri Lanka	Galle	1997-2004	Day & night	1, 3	(11, 77)
Indonesia	Segara Anakan	2004-2006, 2014-2016	Day	1, 2, 3	(78, 79)
Hong Kong	Mai Po	1985-97, 2016-20	Day & night	1, 2, 3	(80, 83)
Hong Kong	Ting Kok	2016-20	Day & night	1, 2, 3	
Hong Kong	Tung Chung	2016-20	Day & night	1, 2, 3	
Australia	Moreton Bay	2000-2002, continued to 2017	Day & night	1, 2, 4	