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

Stefano Cannicci[a,b], Shing Yip Lee[c,d,1], Henrique Bravo[a,e], Jaime Ricardo Cantera-Kintz[f], Farid Dahdouh-Guebas[g,h], Sara Fratini[b], Marco Fusi[i,j], Pedro J. Jimenez[a], Inga Nordhaus[k,l], Francesca Porri[m,n], and Karen Diele[j]

aDivision of Ecology and Biodiversity, Swire Institute of Marine Science, The University of Hong Kong, Hong Kong SAR; bDepartment of Biology, University of Florence, 50019 Sesto Fiorentino, Italy; cAustralian Rivers Institute, Griffith University Gold Coast, Southport, QLD 4222, Australia; dSimon F.S. Li Marine Science Laboratory, School of Life Sciences, The Chinese University of Hong Kong, Hong Kong SAR; eGroningen Institute for Evolutionary Life Sciences, University of Groningen, 9700 AB Groningen, The Netherlands; fDepartment of Biology, Institute of Marine Sciences and Limnology, University of Valle, Cali 76001, Colombia; gLaboratory of Systems Ecology and Resource Management, Université Libre de Bruxelles, B-1050 Brussels, Belgium; hLaboratory of Plant Biology and Nature Management, Ecology and Biodiversity, Vrije Universiteit Brussel, B-1050 Brussels, Belgium; iDivision of Biological and Environmental Sciences and Engineering, Red Sea Research Centre, King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia; jSchool of Applied Sciences, Edinburgh Napier University, Edinburgh EH11 4BN, United Kingdom; kDepartment of Ecology, Leibniz Centre for Tropical Marine Research, 28359 Bremen, Germany; lDepartment of Communication and Research, Lower Saxon Wadden Sea National Park Authority, 26382 Wilhelmshaven, Germany; mSouth African Institute for Aquatic Biodiversity, Grahamstown 6140, South Africa; and nDepartment of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

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 ($\Delta+$), functional richness (FRi), functional redundancy (FRe), and functional vulnerability (FVu) to assess functional integrity. $\Delta+$ 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.

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. 3D).

Taxonomic distinctness fits best in a logarithmic relationship with the total number of species recorded (Fig. 3A). 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. 3A). 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. 3C). In contrast, a strong relationship between the number of species and FRe is evident (Fig. 3B), while there is only a weak relationship between FRe and FRi (Fig. 3E).

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,
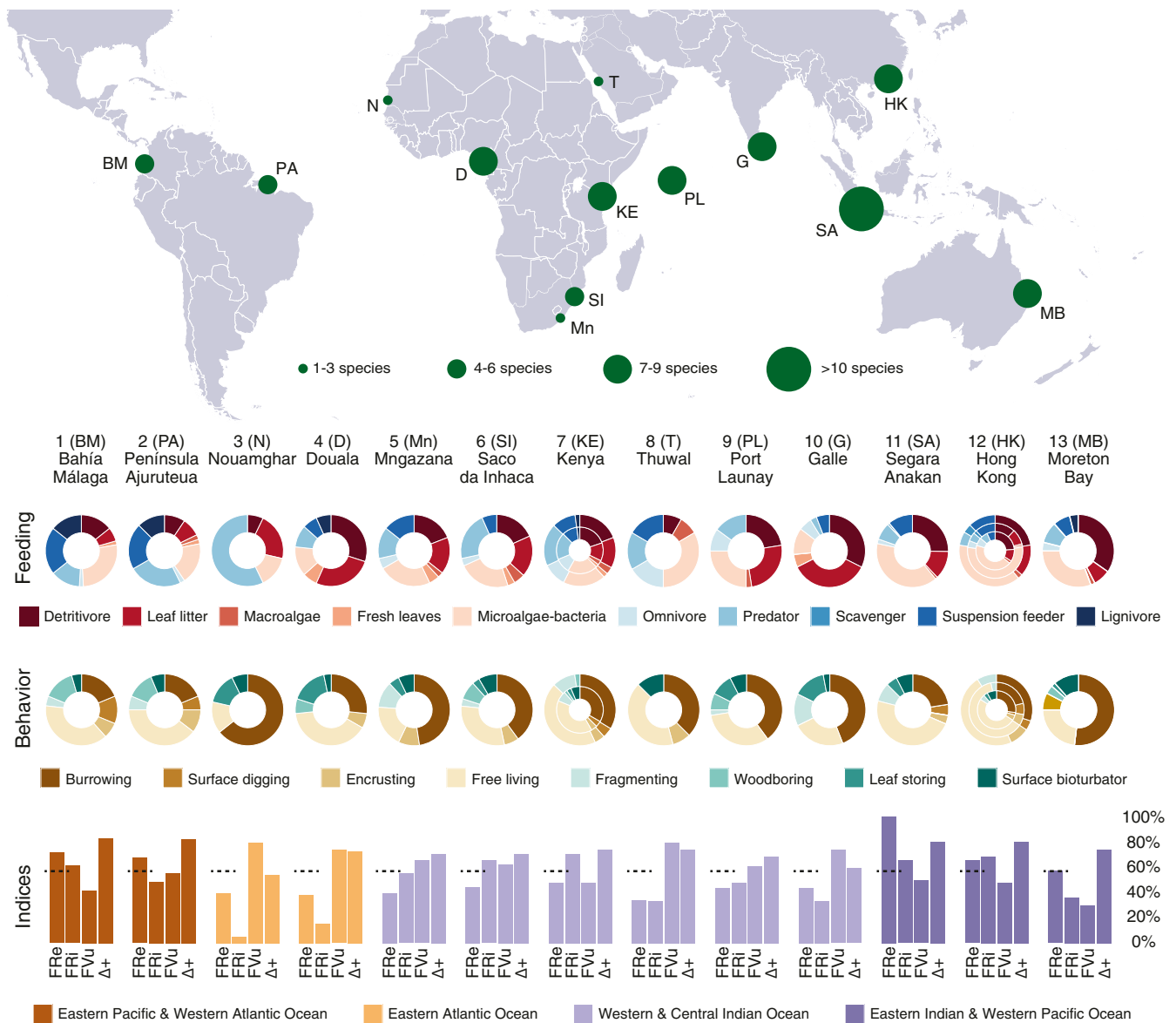
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Fig. 1. Representation of the 16 sampling locations across the globe with their macrofaunal descriptors (data for crustaceans and mollusks pooled) and range of mangrove tree species richness. The tree species richness at each sampling study location 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
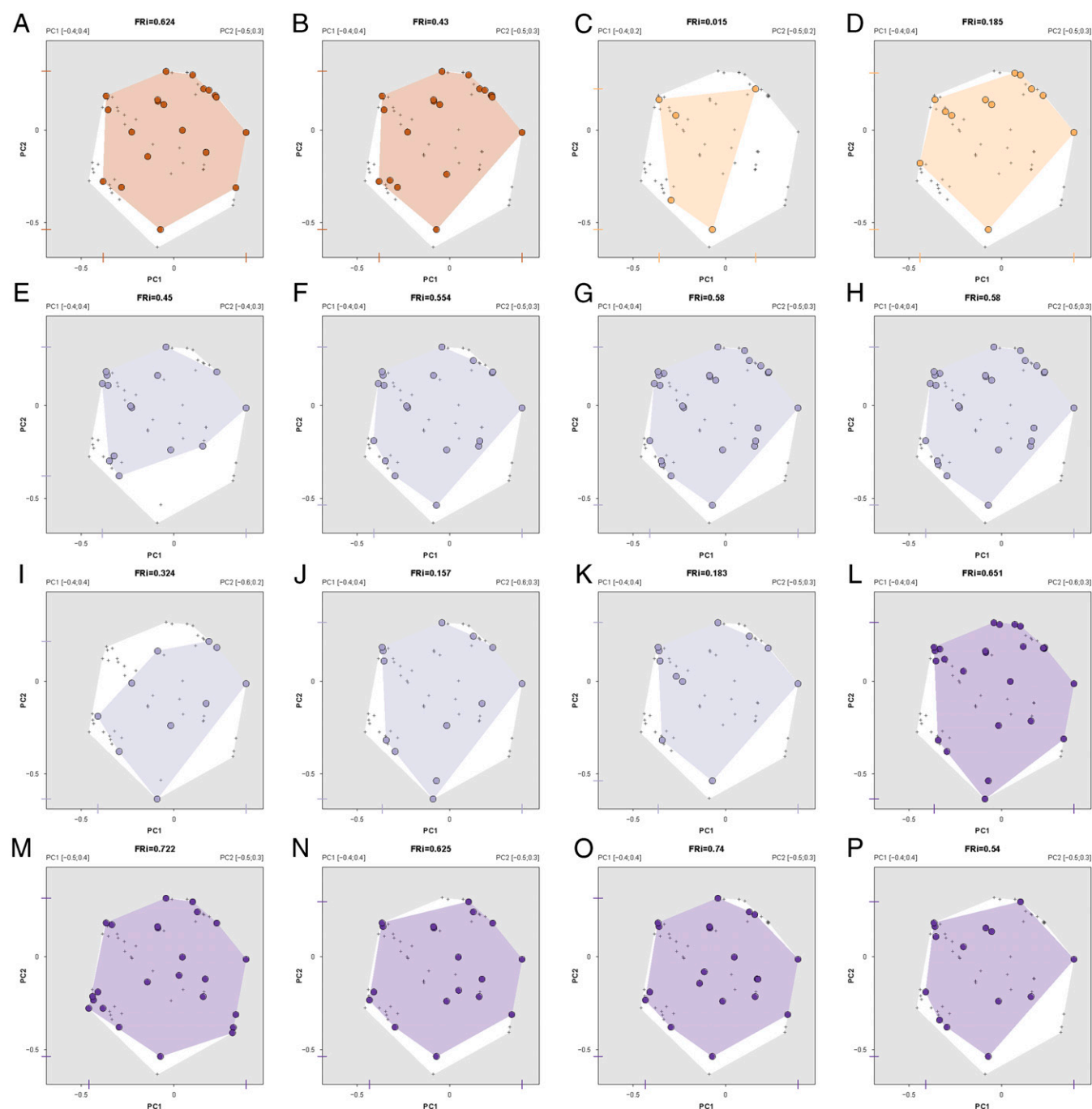
Fig. 2. Principal component analysis graphs representing the FRi (colored area) at the different study locations in relation to the overall functional space (white area) occupied by the total amount of species identified in this study. Species that are present in a specific location are highlighted with 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
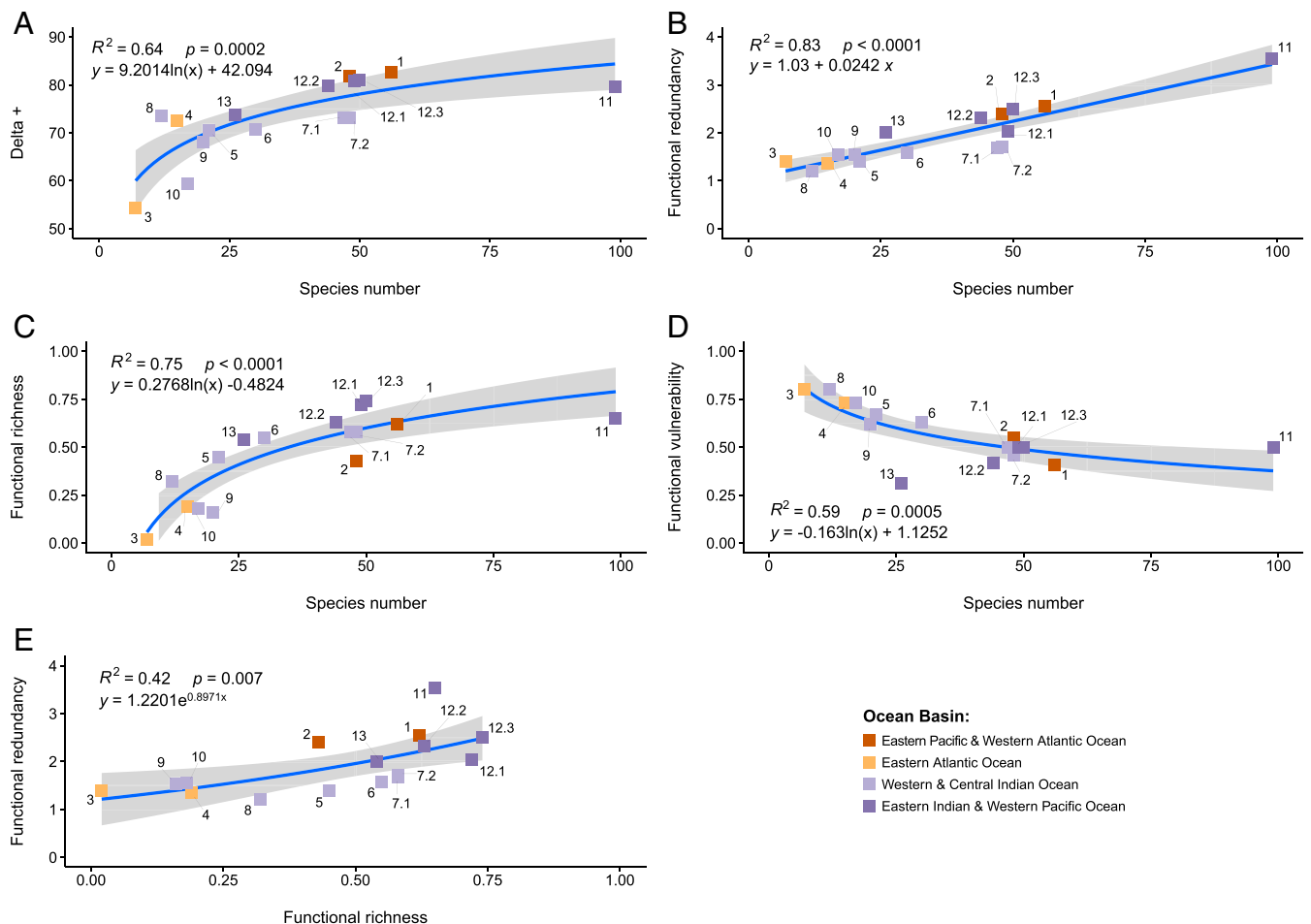
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Fig. 3. Relationships among number of macrobenthic species recorded (see Fig. 1 for key to locations) and the computed taxonomic and functional indices. Best fitted trend lines (dotted blue line) and the associated R^2 value are shown for (*A*) taxonomic 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) $FRe = \frac{S}{FE}$							
	Mangrove invertebrate fauna (this study)	Corals (55)	Benthic marine biota (56)			Reef fishes (17)	Reef fishes (36)	Reef fishes (57)	Lichens (58)	Freshwater fishes (59)
			Cambrian	Silurian	Modern					
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	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 macro-benthic 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, macro-algal 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),

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

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

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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