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# The core mangrove microbiome reveals shared taxa potentially involved in nutrient cycling and promoting host survival

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## Abstract

**Background** Microbes have fundamental roles underpinning the functioning of our planet, they are involved in global carbon and nutrient cycling, and support the existence of multicellular life. The mangrove ecosystem is nutrient limited and if not for microbial cycling of nutrients, life in this harsh environment would likely not exist. The mangroves of Southeast Asia are the oldest and most biodiverse on the planet, and serve vital roles helping to prevent shoreline erosion, act as nursery grounds for many marine species and sequester carbon. Despite these recognised benefits and the importance of microbes in these ecosystems, studies examining the mangrove microbiome in Southeast Asia are scarce.cxs

**Results** Here we examine the microbiome of *Avicenia alba* and *Sonneratia alba* and identify a core microbiome of 81 taxa. A further eight taxa (*Pleurocapsa*, *Tunicatimonas*, *Halomonas*, *Marinomonas*, *Rubrivirga*, *Altererythrobacte*, *Lewinella*, and *Erythrobacter*) were found to be significantly enriched in mangrove tree compartments suggesting key roles in this microbiome. The majority of those identified are involved in nutrient cycling or have roles in the production of compounds that promote host survival.

**Conclusion** The identification of a core microbiome furthers our understanding of mangrove microbial biodiversity, particularly in Southeast Asia where studies such as this are rare. The identification of significantly different microbial communities between sampling sites suggests environmental filtering is occurring, with hosts selecting for a microbial consortia most suitable for survival in their immediate environment. As climate change advances, many of these microbial communities are predicted to change, however, without knowing what is currently there, it is impossible to determine the magnitude of any deviations. This work provides an important baseline against which change in microbial community can be measured.

**Keywords** Bacteria, Blue carbon, Conservation, Dimethylsulfoniopropionate (DMSP), Ecosystem services, Microbial ecology, Southeast Asia

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## Background

Mangrove trees occupy a transitional zone between marine and terrestrial environments, and are the only tree species on the planet that can thrive in the saline, oxygen limited habitat found in this habitat [1–4]. These highly productive ecosystems are found in tropical and subtropical regions where they have significant ecological and economic importance. They are critical for nutrient cycling, provide basal organic matter to coastal food webs, preventing coastal erosion, filtering pollutants, are biodiversity hotspots, and act as nurseries for many marine animals [5–8]. Economically, they buffer against natural disasters, support coastal fisheries, and are the source of many forestry products [8, 9].

Microorganisms have key roles in mangrove ecosystems, and are important in promoting growth and maintaining productivity [10–13]. These microbes contribute significantly to carbon cycling and the global carbon budget [14]. Despite their limited area, accounting for only approximately 3% of global forest cover, mangroves are significant carbon sinks with estimates suggesting they contain 10% of all global carbon emissions [15–17]. Known as “blue carbon”, mangroves are able to sequester atmospheric carbon dioxide in above and below ground structures (e.g., leaves and roots etc.). Ultimately, this carbon becomes locked in the anoxic sediments where it remains stable until disturbed [17, 18]. Once disturbed, usually through anthropogenic factors such as habitat clearance or modification, microbial processes can release this carbon back into the atmosphere where it contributes to climate change [19, 20]. However, despite the growing interest in blue carbon, we currently lack a detailed understanding or characterisation of the microbial communities and potential drivers involved in biogeochemical cycling in these coastal ecosystems [21], particularly in Southeast Asia. As climate change progresses and coastal habitats are further degraded by land-use change, eutrophication, and other anthropogenic activities, many of these coastal ecosystems are predicted to become net sources of carbon instead of sinks [19, 20, 22–26]. Consequently, mangroves and other coastal habitats, along with their associated blue carbon stocks, are unlikely to fulfil their claimed potential as nature-based climate solutions, with many of their benefits likely overstated, especially in the light of continued habitat degradation [18, 27–31]

The importance of the microbiome in maintaining and promoting host health has been recognised in many organisms in both terrestrial and marine environments [32–37], and the role of the microbiome in promoting plant growth and resilience in terrestrial ecosystems is well established [38, 39]. However, the ecological importance of the coastal microbiome is not yet

well-understood, although several studies have shown that fungal and bacterial diversity are key to habitat restoration in marine environments [5, 8]. Several mangrove-associated bacteria are known to promote root growth, support nutrient cycling and availability, degrade contaminants, and aid in other essential processes [5, 7, 40–42]. Despite this recognised importance, the dynamics, distribution, and community composition of microbes in mangrove and coastal ecosystems remain vague [10, 11, 43]. This paucity is particularly acute in Southeast Asia (but see [44, 45] for relevant work on seagrasses).

Thirty-four percent of global mangrove cover is found in Southeast Asia, with Indonesia and Malaysia having the largest area of mangrove forest in the region [46–48]. Mangroves in Southeast Asia are typically highly productive, and are the oldest and most biodiverse mangrove forests in the world [49–51]. Yet, primarily a consequence of anthropogenic activities [52–54], regional rates of loss are some of the highest in the world [48, 55, 56]. Restoration of mangrove ecosystems through strategies such as out-planting of nursery-raised saplings, raised bed methods, and direct propagule planting have shown mixed results, with most eventually failing [51, 57–60]. However, greater success has been achieved when inoculation with local bacterial and fungal species has been performed [5] and the matching of microbial communities between transplant and out-planting sites to mitigate host maladaptation to a new environment has been recommended [61, 62]. Given that microbial communities frequently show distinct compositions, even across comparatively small spatial scales, an understanding of this community structure should be an important consideration in future restoration activities [63–67].

The idea of a ‘core microbiome’ was initially explored by the Human Microbiome Project, and was defined as a group of microbial taxa that are shared by all, or most humans [68]. The ubiquity of these taxa in their host species led to the suggestion that this core microbiome may play an important role in maintaining host biological function [69], and in natural ecosystems, these ubiquitous microbes have similarly been hypothesised to be critical for overall ecological functioning [70, 71]. Here we examine the microbiome of two widespread mangrove species, *Sonneratia alba* and *Avicennia alba* throughout the Malay Peninsula. We hypothesise that a ‘core mangrove microbiome’ of shared microbial taxa will exist between both species. More generally, despite sharing a core taxa of microbes throughout the region and between species, we expect to identify microbial community differentiation between species, geographic locations and structure sampled.

Studies such as this are an important step in understanding the Southeast Asian mangrove microbiome,

they allow us to generate baseline data on the associated microbial communities. These communities are predicted to change under future projected climate change scenarios [72], but it is impossible to assess the magnitude of these changes, or the taxonomic shifts that will occur without knowing what microbes are present and their spatial structure. As interest in mangrove restoration increases throughout the region, an understanding of the microbes associated with these habitats will become an increasingly important consideration in conservation initiatives, especially as we gain further insights into the vital roles microbes play in promoting and sustaining host health.

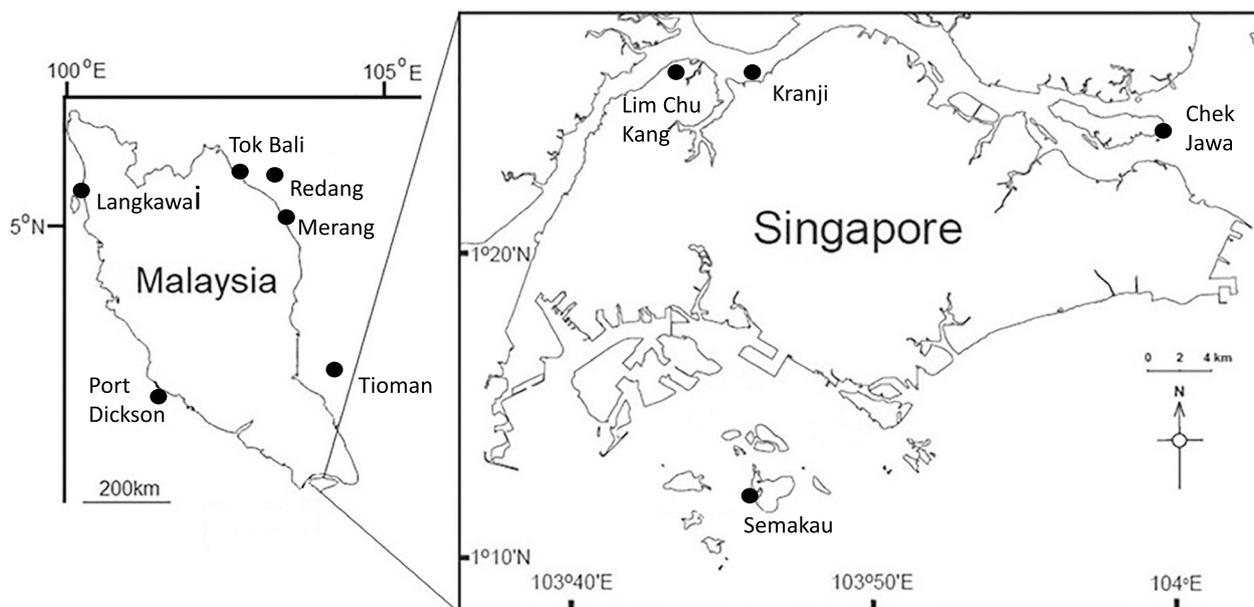
## Methods

At each of nine sampling locations throughout Singapore and Malaysia, we targeted 10 visibly healthy whole leaves, fruiting bodies (mangrove fruit) and entire pneumatophores from *Avicennia alba* and *Sonneratia alba*. In addition to living tissue, a sediment sample was collected in close proximity to each tree (< 1 m), with sediment samples taken from approximately 4 cm below the surface. We were unable to find *Avicennia alba* at two sample locations in Malaysia (Port Dickson, and Tioman) (Fig. 1). For both species, DNA was extracted with a Qiagen DNeasy PowerSoil Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Prior to extraction all samples were disrupted in an Omni Bead Ruptor 24 (Omni International, Kennesaw, GA, United States) at  $8 \text{ ms}^{-1}$  for 2 min. PCR amplification targeting the V4

region of the 16S small sub-unit (SSU) rRNA gene was performed using the 515F and 806R primers modified to include Illumina adaptors, a linker and a unique barcode [73]. All reactions were performed in a total volume of 25  $\mu\text{l}$ , containing 1  $\mu\text{l}$  of undiluted template, 0.1  $\mu\text{l}$  of KAPA 3G Enzyme (Kapa Biosystems, Inc, Wilmington, MA, USA), 0.75  $\mu\text{l}$  of each primer at 10  $\mu\text{M}$ , 2.5  $\mu\text{l}$ , 1.5  $\mu\text{l}$  of 1.5  $\text{mg ml}^{-1}$  BSA, 12.5  $\mu\text{l}$  KAPA PCR Buffer and water to 25  $\mu\text{l}$ . PCR cycling was 94  $^{\circ}\text{C}$  for 180 s, followed by 35 cycles of 94  $^{\circ}\text{C}$  for 45 s, 50  $^{\circ}\text{C}$  for 60 s and 72  $^{\circ}\text{C}$  for 90 s, and a final extension at 72  $^{\circ}\text{C}$  for 10 min. Negative extraction and PCR controls were included to identify any potential contamination issues. Prior to pooling for sequencing, normalisation and cleaning of PCR products was performed in SequalPrep normalisation plates following all manufacturer instructions (Invitrogen). Sequencing was carried out on the Illumina MiSeq platform (600 cycles, V3 chemistry, 300 bp paired end reads) with a 30% PhiX spike (Macrogen).

## Bioinformatics and statistics

For full details of sequencing statistics and numbers of reads remaining after quality control and filtering, see Additional file 1: Tables S1 and S2. Barcodes and adaptors were removed from de-multiplexed sequence files using *Cutadapt* version 3.4 [74]. All analysis performed in R used version 3.4.1 (R Core Team, 2017). Reads were filtered based on quality scores and trimmed using the *DADA2* package version 1.9.0 [75, 76]. Forward reads were truncated at 300 bp, and reverse reads were



**Fig. 1** Map indicating sampling locations

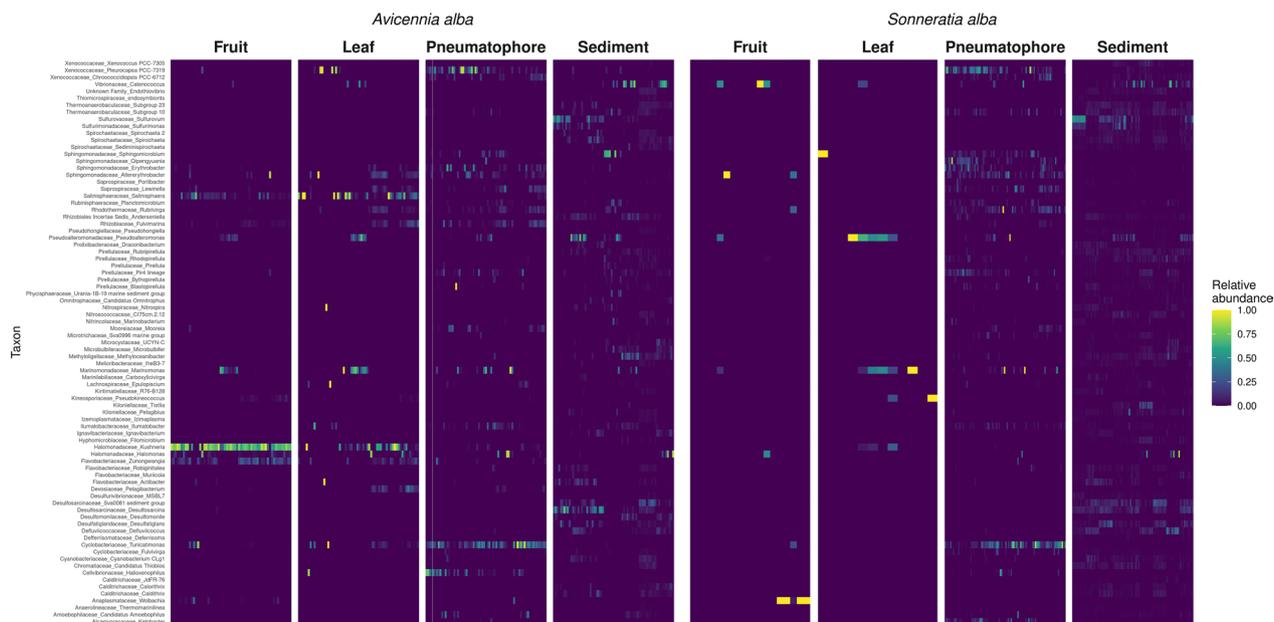
truncated at 200 bp. Both forward and reverse reads were filtered to remove any reads less than 100 nucleotides long, or with a max EE (expected error) of 2, and reads were additionally truncated at the end of ‘a good quality sequence’ with the parameter truncQ=2. The *DADA2* algorithm was next used to estimate error rates from all quality-filtered reads and then to merge forward and reverse reads and infer amplicon sequence variants (ASVs). Chimeras were removed with de novo detection. Sequenced extraction and PCR negatives were used to identify possible contaminants using the *decontam* R package [76], and remaining ASVs were assigned taxonomy with the RDP classifier [77] against a training set based on the Silva v132 16S database [78]. Phylogenetic placement of ASVs was assigned by aligning sequence variants without an anchor using the *AlignSeqs()* function of the *decipher* R package version 2.6.0 [79] and constructing a maximum likelihood tree with the *optim.pml()* function from an initial starting tree built using the *NJ()* function in the *phangorn* R package version 2.4.0 [80].

Any ASVs assigned to mitochondrial or chloroplast identities were removed. Raw sequence counts were then converted to relative abundance data. Alpha diversity metrics for each location were calculated, and non-metric multi-dimensional scaling (NMDS) was performed on the UniFrac [81] dissimilarity matrix of samples using *vegan* version 2.6–4 [82] and *phyloseq* version 1.41.1 [83] R packages (Fig. 2). Permutational multivariate analysis of variance (PERMANOVA) (Additional file 1: Table S3)

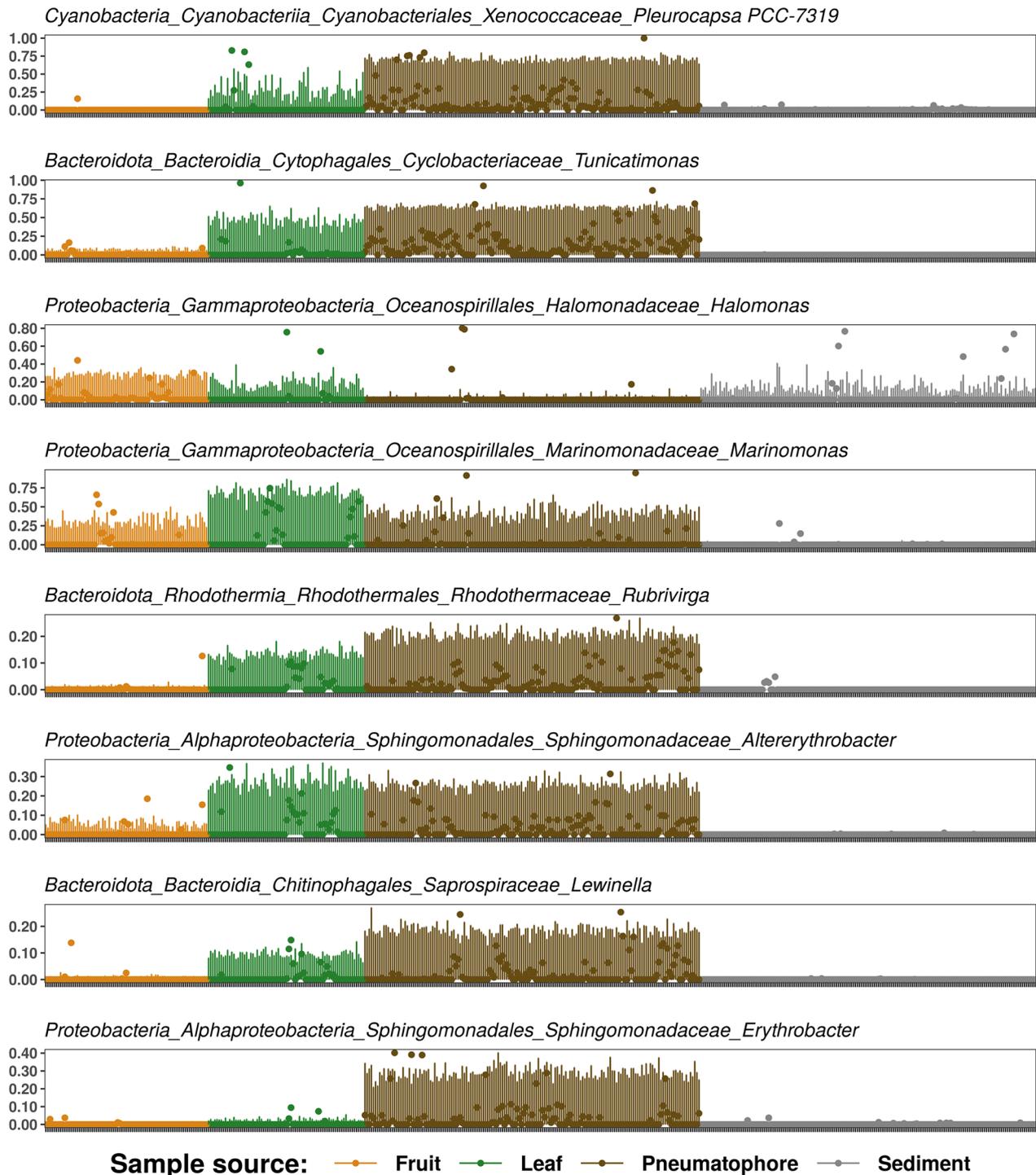
was performed on the ASV table with ‘location’ and ‘plant structure’ as predictors using the *adonis()* function of the *vegan* package. A Mantel test with 999 permutations was performed using the *vegan* R package. Differential abundance analyses were performed using the *vegan*, *indicspecies* version 1.7.12 [84] and *corncob* [85] R packages. ASVs and species-level taxa that were detected by all three methods as being differentially abundant in various mangrove structures are reported below. The *microbiome* R package version 1.10.0 was used to detect a core taxa (Lahti et al. 2017) (Fig. 3). Here we define core taxa as those present in at least 20% of the samples at a relative abundance of at least 10% in each of those samples (i.e., those taxa making up at least 10% of the reads in at least 20% of all samples. These thresholds are inherently arbitrary [86] but were informed by abundance-occupancy distributions [87]. All sequences associated with this work have been deposited at the National Center for Biotechnology Information under BioProject ID: PRJNA735404.

**Results**

In total, sequencing generated 28,297,986 and 29,484,815 reads for *Avicennia alba* and *Sonneratia alba* respectively. After quality control processing and chimera removal, 4,835,163 reads for *A. alba* and 13,861,503 reads for *S. alba* remained and were used in all downstream analysis (Additional file 1: Tables S1 and S2). The *A. alba* and *S. alba* libraries used in downstream analysis contained a mean of 17,330 (median=12,785) and 38,944



**Fig. 2** Heatmap showing the abundance of each of the 81 core taxa identified in each species and sampled part



**Fig. 3** Corncob plot indicating differential abundance of each of the eight taxa identified using three different techniques. Plot only shows the results of *corncob* analysis. Dots represent model coefficients associated with relative abundance and lines represent 95% prediction intervals for the observed relative abundance (dispersion)

(median = 38,504) reads per sample respectively, with 12,720 and 24,347 unique ASVs found in each respective library. Rarefaction curves for both species indicate that

sufficient sequencing depth was achieved with all samples reaching asymptote (Additional file 1: Fig. S1).

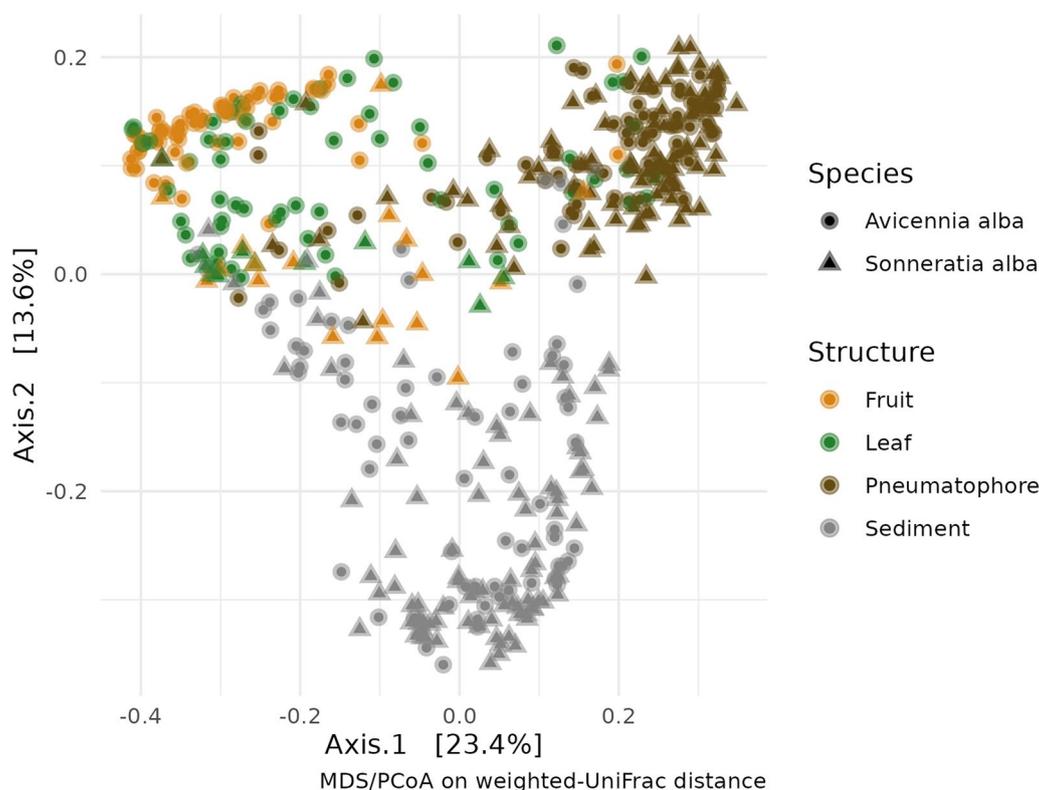
A core microbiome consisting of 81 taxa was identified in both species throughout all samples (Fig. 2).

Differential abundance analysis was performed using *simper* in *vegan*, *indicspecies* and *corncob*. Eight bacterial taxa were identified as differentially abundant between mangrove parts by all three methods. These differentially abundant taxa were *Pleurocapsa*, *Tunicatimonas*, *Halomonas*, *Marinomonas*, *Rubrivirga*, *Altererythrobacter*, *Lewinella*, and *Erythrobacter* (Fig. 3). These taxa are key degraders of important marine carbon compounds such as formaldehyde, gelatine, and agar (See discussion), and their significant enrichment in living mangrove parts over sediment (Fig. 3) highlights how important mangroves are as habitats for ecologically critical taxa. PERMANOVA (Additional file 1: Table S3) indicates a weak but significant difference in bacterial communities between host species ( $p=0.001$ ,  $R^2=0.015$ ), with sampled plant part and sampling location having a larger influence on community structure ( $p=0.001$ ,  $R^2=0.197$ ; &  $p=0.001$ ,  $R^2=0.097$  respectively). This pattern is also evident in the NMDS plot (Fig. 4) with samples of the same type (e.g., leaves) tending to cluster together irrespective of the host species. Above ground parts (leaves and fruits) tend to be similar while sediment and pneumatophores host bacterial communities that are distinct from each other, the leaves, and the fruits. Further confirming this similarity, plots of beta-dispersion indicate a

high degree of overlap in microbial communities between species (Additional file 1: Fig. S2) and between fruits and leaves, while pneumatophores and sediment samples tend to be more dissimilar (Additional file 1: Fig. S3). The highest bacterial diversity was found in sediment samples. In living tissues in both mangrove species, pneumatophores contained the highest diversity, while leaves and fruits showed similar diversity (Additional file 1: Fig. S4). A Mantel test indicated a significant pattern of distance decay of similarity in microbial communities (999 permutations; Mantel statistic  $r: 0.1097$ ;  $p=0.001$ ).

## Discussion

Consistent with other work examining microbial community structure in a variety of host taxa, we show that microbial community structure exists around the Malay Peninsula [44, 45, 61, 64, 88, 89], and this structure is primarily a consequence of plant part examined, location sampled, and host identity. It is likely that these differences are driven by local environmental conditions, with locations closer together tending to have more similar environmental conditions in comparison to those that are more geographically distant. This hypothesis is further supported by the significant pattern of distance decay of similarity we observe in microbial communities,



**Fig. 4** Weighted-UniFrac distance ordination for both species studied and all sampled parts, including sediment

meaning that communities are more similar when spatial distance between them is low, a consequence of the host's ability to exert a degree of control over the composition of their microbial communities, tailoring them to local conditions [90, 91]. Given these findings, and the recognised high rates of failure in mangrove restoration programmes, explicit consideration of microbial communities could help to improve success [92]. More so since inoculation with bacterial and fungal species found in the local environment has already been shown to improve restoration success and promote tolerance to stress [5, 67, 93].

We identified a core *Avicennia alba* and *Sonneratia alba* mangrove microbiome consisting of 81 taxa. Given the ubiquity of these taxa in both species and in all living parts (e.g., leaves and pneumatophores) it is likely they play a key role in mediating host fitness. For example, mangroves are nitrogen-limited environments, and in general are considered as nutrient-deficient habitats [94–96]. Correspondingly, a number of the taxa we identified in the core microbiome are involved in nitrogen cycling (e.g., *Nitrospiraceae nitrospira*, *Rhizobiales Incertae Sedis Anderseniella*, *Rhizobiaceae fulvimarina*) and thus help promote growth in what would otherwise be a challenging environment for plant life. Similarly, the core microbiome in this work contains a number of taxa involved in sulphur cycling (e.g., *Sulfurimonadaceae sulfurimonas* & *Sulfurovaceae sulfurovum*). The bacterial oxidation of sulphur can improve substrate fertility and aid in the removal of toxic sulphide that is produced by sulphur-reducing bacteria [97, 98]. These core taxa would be a good starting point for further investigation as potential inoculates that could improve restoration success, especially when transplants are grown *ex-situ*. However, increasingly evidence is also suggesting that rare taxa are likely to be just as important [69] and may play important roles in allowing hosts to survive in challenging environments, or in helping facilitate adaption to geographically unique environmental conditions. This is especially true in biogeochemical cycles and in protecting hosts from pathogens [99, 100].

We identified eight bacterial taxa shared between both species that are differentially abundant (Fig. 3). These eight were primarily enriched in living parts suggesting that they play an important role in the Southeast Asian mangrove microbiome. *Pleurocapsa*, a nitrogen fixing cyanobacteria [101] is enriched within pneumatophores, and it is likely that members of this group facilitate nitrogen uptake in the water-logged and nutrient-limited mangrove sediments.

Members of the Bacteroidetes genus *Tunicatimonas* (here, enriched in pneumatophores) were first isolated from sea anemones [102] and have since been identified

as common on plastic debris in marine environments where they are thought to be well adapted to take advantage of the new niches this plastic creates [103]. While *Tunicatimonas* might not serve any purpose in promoting host health, their increased abundance could be a consequence of plastic pollution. Plastic pollution is a recognised problem in Southeast Asia, and much of this plastic can become entangled within mangroves where it can disrupt growth and lead to ecological instability [104, 105]. We hypothesize that plastic debris could be facilitating the transport of *Tunicatimonas* into mangrove ecosystems, particularly since *Tunicatimonas* taxa are found enriched on pneumatophores, a structure ideally suited to trapping plastic debris.

*Halomonas* spp. (here, enriched in sediment, fruits, and leaves) have previously been identified in Southeast Asian mangroves where they produce the compound ectoine [106]. This compound is able to stabilize proteins and other cellular structures in the presence of high intensity UV irradiation, heat stresses (cold and high), fluctuations in pH and can help hosts survive extreme osmotic stress [106, 107]. Members of this genus are most enriched in the above ground structures—those that are exposed to the extreme levels of UV light that are frequently encountered in tropical habitats suggesting that they could play a protective role in these parts.

The genus *Marinomonas* (here, enriched in all living plant tissues) is abundant in marine ecosystems where it is implicated in melanin synthesis and the catabolism of dimethylsulfoniopropionate (DMSP) to dimethyl sulfide (DMS). DMSP metabolisers are acknowledged as important constituents of the coral microbiome where they have principal roles in sulphur cycling, pathogen suppression and mediating thermal stress responses [37, 88, 108–110]. The same properties that make DMSP metabolisers beneficial microorganisms in coral mean that this group warrants further investigation in mangroves, particularly as they are enriched in both species. Additionally, this genus is known to degrade agar, a very abundant and recalcitrant carbon compound produced by marine algae.

Little is known of the *Rubrivirga* genus (here, enriched in leaves and pneumatophores), however, they are described as chemoorganotrophs [111] meaning they are able to oxidise organic chemicals to produce energy. Therefore, they are likely to be involved in nutrient cycling and this genus would be a good candidate for further investigation into its role in the mangrove microbiome.

Similarly, details on *Altererythrobacter* (here, enriched in leaves and pneumatophores) are scarce, with no information on the specific functions they perform, but they have been isolated from mangrove ecosystems previously

[112, 113] and are known to degrade formaldehyde. This ubiquity suggests they have an important role in the mangrove microbiome and would be a good target for further study.

*Lewinella* (here, enriched in leaves and pneumatophores) are halotolerant heterotrophs that are commonly encountered in activated sludge and are able to break down complex molecules [114] abundant in marine habitats such as gelatine [115]. They show increased abundance when coastal areas undergo sudden vegetation declines that can result from land-use change [116]. Further investigation of this genus may make it possible to identify indicator species that can be used in the design of customised management and conservation strategies.

*Erythrobacter* (here, enriched in pneumatophores) have been isolated from mangrove habitats in multiple studies throughout the world [95, 117–119], and is known to degrade complex molecules such as formaldehyde [120], but little is known about their functions in these habitats. Like *Altererythrobacter*, the ubiquity of *Erythrobacter* in multiple mangrove forests suggests that they play an important role in the mangrove microbiome, and again this genus would be a worthy candidate for future studies trying to determine whether beneficial mangrove microbes exist.

Despite having a shared core of 81 taxa across all living parts, each part does host a significantly different bacterial community. In both species, leaves and fruiting bodies, or above ground structures have a similar diversity, and of the living parts, the pneumatophore has the most diverse microbial community. Similar to other studies, the highest diversity of microbes is seen in sediment samples [44, 45, 65, 66]. Our ordinations further support these observations with fruit and leaves having similar microbial communities and therefore clustering together, while pneumatophores and sediment samples form well-defined and clearly differentiated clusters. In all cases, the microbial communities from the same species, in the same sampled part (e.g., *A. alba* and *S. alba* leaves) appear similar and do not form distinct clusters. This similarity corroborates the high number of shared core taxa between both species.

Among the eight taxa found to have significantly different abundance, all but one (*Halmonas*) exhibited strong preference for mangrove plant components over sediment (Fig. 3). This indicates that these potentially important taxa depend on mangroves for their persistence in the coastal environments of Southeast Asia, and further highlights the importance of mangroves for fostering microbial diversity and hosting bacterial taxa that play key roles in nutrient cycling.

Microbes have fundamental roles in the cycling of many elements, and are major regulators of greenhouse

gasses [121]. Climate change will alter how these microbial communities are structured [19, 20, 24, 26], and experimental manipulations show that 4 °C of warming can increase soil respiration by as much as 37%, with much of this increase mediated by microbial decomposition of sequestered carbon [24]. Under the anticipated future climate change scenarios, much of the carbon stored in coastal ecosystems will become vulnerable to increased microbial decomposition, and mangrove ecosystems will likely move from net sinks to net sources of greenhouse gasses. Given this, it is crucial that we understand how mangrove microbial communities are currently assembled and structured in order to determine how best to keep existing carbon stores intact.

The arguments in favour of mangrove restoration to increase biodiversity are unequivocal. However, things are much less clear when it comes to blue carbon and how climate change and restoration will impact greenhouse gas fluxes in coastal ecosystems [122–124]. Anecdotally, the consensus suggests that restoration will aid in the sequestering of atmospheric carbon. Unfortunately, scientific surveys of greenhouse gas fluxes in restored habitats show that CO<sub>2</sub> fluxes in these ecosystems have actually increased. These post restoration increases are observed in numerous coastal ecosystems (e.g., mangroves, kelp forests, saltmarshes and seagrasses) [27, 31, 116, 125–127] and demonstrate the challenges involved when trying to understand greenhouse gas fluxes in these ecosystems. These challenges underline the need for studies such as this, without them we will not know what microbes are present or how they will change.

## Conclusion

This work uncovers a core mangrove microbiome and identifies a more limited set of eight microbial taxa that are differentially abundant in different compartments in both species of mangroves surveyed. Their elevated abundance suggests possible beneficial properties that could improve restoration success, given this; these would be good candidate taxa for further screening to determine what, if any benefits hosts could derive from their associations with them. Importantly, this work provides a baseline that can be used to measure changes in microbial community structure against, this is valuable because it is predicted that these communities will change in response to climate change. However, it is impossible to assess the magnitude or direction of these changes without knowing what is currently present in the mangrove microbiome.

Natural systems are complex, and if all the factors involved in carbon sequestration and its cycling through mangrove ecosystems are not fully considered, especially how the predicted changes in microbial communities as

the climate warms impact CO<sub>2</sub> flux, it is possible that we will do more harm than good. Particularly when it comes to using coastal ecosystems in carbon trading schemes and in the offsetting of emissions.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40793-023-00499-5>.

**Additional file 1.** Supplementary material.

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## Author contributions

Study conception and design, BJW. Sample collection, BJW, JNL. Laboratory work BJW. Analysis, BJW, TM, LB, KH, LS, ZYY, GZ. First draft, BJW, GZ. All authors commented and contributed to improving the manuscript and preparing the manuscript for submission. All authors read and approved the final manuscript.

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## Availability of data and materials

All data associated with this work has been deposited at the National Center for Biotechnology Information under BioProject ID: PRJNA735404. All code for downloading, processing, and reproducing analyses is provided as a versioned GitHub release at: <https://zenodo.org/record/7802402#.ZDdnjvZByUK>.

## Declarations

### Ethics approval and consent to participate

Not required.

### Consent for publication

Not required.

### Competing interests

The authors declare no competing interests.

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