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Exceptional but vulnerable microbial diversity in coral reef animal surface microbiomes

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Abstract :

Coral reefs host hundreds of thousands of animal species that are increasingly threatened by anthropogenic disturbances. These animals host microbial communities at their surface, playing crucial roles for their fitness. However, the diversity of such microbiomes is mostly described in a few coral species and still poorly defined in other invertebrates and vertebrates. Given the diversity of animal microbiomes, and the diversity of host species inhabiting coral reefs, the contribution of such microbiomes to the total microbial diversity of coral reefs could be important, yet potentially vulnerable to the loss of animal species. Analysis of the surface microbiome from 74 taxa, including teleost fishes, hard and soft corals, crustaceans, echinoderms, bivalves and sponges, revealed that more than 90% of their prokaryotic phylogenetic richness was specific and not recovered in surrounding plankton. Estimate of the total richness associated with coral reef animal surface microbiomes reached up to 2.5% of current estimates of Earth prokaryotic diversity. Therefore, coral reef animal surfaces should be recognized as a hotspot of marine microbial diversity. Loss of the most vulnerable reef animals expected under present-day scenarios of reef degradation would induce an erosion of 28% of the prokaryotic richness, with unknown consequences on coral reef ecosystem functioning.

Keywords : skin microbiota, phylogenetic diversity, conservation, marine biodiversity, Octocorallia, Scleratinia

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BACKGROUND

Coral reefs provide habitats for at least 500,000 multicellular species [1], including more than 6,000 described fish and 1,000 coral species [2,3]. These animals are covered by diverse and abundant microbes (*Bacteria, Archaea*, viruses and micro-eukaryotes) which all together constitute the surface microbiome [4]. Animal surface microbiomes play crucial roles for their hosts, contributing to host resistance to pathogens and environmental perturbations [5,6], and to assimilation of nutrients [4]. However, animal surface microbiomes have been assessed in less than 50 and 100 coral and fish species, respectively [4,6–10].

Large scale surveys of the marine water column demonstrated the important diversity of planktonic marine microbes [11,12]. However, these planktonic microbes are compositionally distinct from marine animal surface microbiomes, and many animal-associated microbes remain undetected in planktonic microbial communities [8,10,13]. In addition, marine animals have diverse biological traits that provide specific habitats at their surface, which ultimately favours the proliferation of microbial lineages that are different among different species [7]. Surface microbiomes and planktonic microbes form a microbial 'metacommunity' [14], where local communities within it (individual animal microbiomes, as well as planktonic communities) are connected by dispersal of microbes through direct contacts and through the water column. Given the distinct composition of animal surface microbiomes between species, and the diversity of animal surfaces inhabiting coral reefs, surface microbiomes may constitute an important part of the coral reef microbial metacommunity. However, the contribution of animal surface microbiomes to the coral reef microbial diversity is currently unknown.

Coral reefs are facing increasing human pressures (including ocean warming, acidification and overfishing; [15,16]) inducing an increased risk of extinction of a significant proportion of animal diversity (up to 8% and 10% of coral and fish species; [16,17]). The documented erosion of animal biodiversity as well as the decrease of animal abundance may result in the loss of their associated microbial species. However, the effect of such erosion on microbial diversity has to date not been assessed.

In this study, we sampled surface microbiomes of abundant coral reef animals (*e.g.* fishes, corals, crustaceans, echinoderms, mollusks and sponges) from the same restricted area over a

short period. In so doing we avoided spatial and/or temporal variation of microbial diversity driven by environmental variability. We sampled the surface prokaryotic microbiome of 265 coral reef animals belonging to 74 different taxa, including 32 and 18 genera of teleost fishes and *Anthozoa* (hard and soft corals, and anemones), respectively, and 12 taxa of crustaceans, echinoderms, mollusks and sponges, from a single coral reef ecosystem (Mayotte lagoon, Indian Ocean). In order to test the hypothesis that surface microbiomes represent a major component of the coral reef microbial metacommunity, we compared the prokaryotic diversity hosted by animals to that of the surrounding planktonic communities. Ultimately, we compared the amount of microbial diversity to global microbial diversity estimates and estimated the erosion of microbes due to human-induced animal exinction.

METHODS

Sampling procedure

Sampling was conducted in November 2015 in Mayotte lagoon shallow (depth <10 meters) barrier and fringing coral reefs (Western Indian Ocean, Supplementary Material SM1-1 and 2). We sampled the most abundant taxa from each of the main animal groups (teleost fishes, *Anthozoa*, crustaceans, echinoderms, mollusks and sponges) within a radius of 50 m around each site (SM1-3 and 4). Sampling procedure is provided in SM1-5. Briefly, we sampled skin microbiome by collecting surface mucus or swabbing.

Fishes were identified at species level. Corals were identified at genus level. Classification of other invertebrates was made at species level when possible (for crustaceans, starfish, urchins and anemones), or at higher taxonomic levels for a few clades (one sea cucumber, comatules, hermit crabs, brittle stars and giant clams) (SM1-4). A total of 138 fishes were sampled across two sites, as well as 82 colonies of hard and soft corals, gorgonians and anemones (referred collectively as *Anthozoa*) belonging to 13 genera of *Scleractinia*, 3 *Octocorallia* (soft corals and gorgonians) and one anemone species. We also sampled 43 individuals of crustaceans, echinoderms, mollusks and sponges. For each of 6 days of sampling, water samples were collected and filtrated to collect prokaryotic plankton as explained in SM1-5. Prokaryotic diversity was assessed using high-throughput sequencing of the V4 hypervariable region of the 16S rDNA gene, as detailed in SM1-5.

Sequence processing and phylogenetic analyses

Sequence reads were processed using the *'DADA2'* R-package version 1.2 and R software

v3.4.3 using script provided in Supplementary Material SM1-6. 7% of the 50,237 constructed ASVs were unclassified at this step. In order to define whether they could potentially correspond to remaining mitochondrial sequences, we mapped them onto the Genbank database (NCBI) using the BLASTn alignment tool. 7% of them showed more than 97% identity with a mitochondrial sequence and were removed before computing further analyses. Sequence number ranged from 7,074 to 56,927 across samples (SM1-4). 7,000 sequences were randomly sub-sampled within each sample in order to correct the uneven sequencing efficiency among samples using "rrarefy" function from '*vegan*' R-package version 2.5-5 [18]. To assess the effect of rarefaction on our results, all subsequent analyses were computed on both rarefied and un-rarefied data. Analyses based on rarefied data are included in the main document, while the ones based on un-rarefied data are included in Supplementary Material SM2. These two approaches provided similar results. Zhang-Huang's coverage estimator [19] was calculated using the *'entropart'* R-package version 1.6-1 [20], using "coverage" function, and averaged 0.982±0.015 across all samples (0.998±0.001 before rarefaction). A phylogenetic tree was obtained by adding the ASV sequences into the *GreenGenes* phylogenetic tree version 13.8 [21] using *SEPP* insertion tool [22] with default parameters.

Assessing microbial biodiversity

The average surface microbiome of each fish species, *Anthozoa* genus, or other invertebrate taxa, was computed as the mean relative abundance of each ASV across individuals from the same taxon (SM1-4). Phylogenetic richness of each community was measured using Faith's PD [23], using "pd" function from *'picante'* R-package version 1.8 [24]. Phylogenetic diversity, taking into account the relative abundance of ASVs, was measured using Allen's index [25] using our own R-function (https://github.com/marlenec/chao, q=1). The evenness of ASVs abundances was measured for each microbial sample using *O* [26], which is robust against richness variation [27].

Phylogenetic dissimilarities between animal taxa was assessed using the unweigthed and weighted versions of Unifrac index (U- and W-Unifrac), computed using *'GUniFrac'* R-package version 1.1 [28] and were visualized using Principal Coordinates Analysis (PCoA) computed using *'ape'* R-package, and boxplots computed using function "boxplot.stats" from *'grDevices'* R-package using default parameters.

Statistical tests

Difference in phylogenetic alpha-diversity between plankton and animal surface microbiomes was tested using Kruskal-Wallis tests (KW, 999 permutations) computed with *'vegan'* R-package. Correlation between fish vulnerability (see "**Vulnerability of microbial diversity"** hereafter) and its associated microbiome diversity was assessed using Spearman's correlation tests ("cor.test") performed on phylogenetic independent contrasts (PIC) calculated on diversity indices, using the fish phylogenetic tree used before [7]. Due to the lower resolution of taxonomic identification of corals in our dataset (at genus level) and the polyphyly of genera in published coral trees [29], it was not possible to compute PIC on scleratinians. Therefore, correlation between coral vulnerability and its associated microbiome diversity was performed using a simple Spearman's correlation test.

Difference in microbial structure between plankton and animal surface microbiomes was tested using permutational multivariate ANOVAs (PERMANOVAs) performed on dissimilarities, using "adonis" function in *'vegan'* R-package and 999 permutations. To test if planktonic communities were more variable than surface-associated communities, a permutation analysis of dispersion (PERMDISP) was performed on both indices among planktonic communities and among animal surface microbiomes using "betadisper" provided in *'vegan'*, with 999 permutations.

Differences between surface microbiomes associated to the three major animal groups (44 teleostean fish species, 17 anthozoan genera and 12 other invertebrates' taxa) were tested using PERMANOVAs. The effect of animal's taxon to its associated surface microbiome was assessed for each animal group (before averaging the microbiome per animal taxon, SM1-3 and 4) using separated PERMANOVAs.

Lastly, in order to identify prokaryotic clades that are different between plankton and animal surface microbiomes, and consistent enriched in all water samples or animal taxa, we performed a LEfSe analysis [30] using water samples and animal taxa as subclasses, with *all-against-all* parameter and p-value threshold for significance of 0.05. Then, to identify biomarkers for each animal group (teleostean fishes, *Anthozoa* and other vertebrates), a LEfSe analysis was performed using these groups as main classes, and the different animal taxa belonging to these groups (fish species, anthozoan genera and other invertebrates' taxa) as subclasses, using the same parameters.

Contribution of surface microbiomes to total microbial diversity

We used two approaches to assess the importance of planktonic *vs*. animal-associated prokaryotic diversity to total coral reef microbial diversity. We first computed the

phylogenetic richness of ASVs that were unique to plankton or to animal surfaces. We then compared the diversity of planktonic and animal surface microbiomes, by randomly picking from 1 to 74 animal taxa and 1 to 35 planktonic samples and then computing the total ASV and phylogenetic richness for each sampling depth. This procedure was performed 100 times. To get a conservative estimation of the total sampled + un-sampled prokaryotic species richness in our dataset, we first curated the ASVs in our dataset, removing all unclassified ASVs that could not match any sequence in Genbank database. The remaining ASVs were then grouped into 97%-identity Operational Taxonomic Units (OTUs) using "pick_otus.py" function provided in QIIME version 1.9 [31], with default de novo *usearch* parameter, and OTUs found in less than 2 animal taxa were removed. We obtained 20,021 OTUs from 37,758 curated ASVs. Then, each animal taxon was considered as an independent sampling unit to count the occurrence of each OTU (*i.e.* the number of sampling units where the OTU was recovered). Estimates of OTU richness were calculated using the estimators provided in '*SpadeR'* R-package [32] using "ChaoSpecies" function and type 2 *incidence frequency* data option.

Vulnerability of microbial diversity

To assess the vulnerability of reef microbial diversity to the loss of macro-organisms, we simulated an extinction scenario combining the effects of global warming and overfishing. Macro-organisms taxa were removed proportionally to their respective vulnerability to heat stress for hard corals, and to habitat loss (due to coral bleaching) *plus* fishing for fishes. Vulnerability of scleractinian coral genera to global warming was based on their bleaching response in the Western Indian Ocean [33]. The genus *Isopora*, for which we had no data, was excluded from the extinction scenario. Similarly, no data was available for non-scleratinian *Anthozoa* and for all other invertebrates. There were therefore excluded from the scenario. Vulnerability to fishing [34] was obtained from Fishbase (http://www.fishbase.org/, 2017). Vulnerability to habitat loss due to global change in coral reefs was computed as in Graham et al. [35] using data from Fishbase.org and expert knowledge for input variables. All vulnerability indices are provided in SM1-7, and the script used to simulate such animal diversity extinction and subsequent losses of microbial taxonomic and phylogenetic diversity is available online (https://github.com/marlenec/MicroErosion).

We assessed the vulnerability of prokaryotic diversity hosted by the 44 fish species and 12 genera of scleractinian corals included in the scenario by simulating loss of the 1 to 100% most vulnerable taxa according to their individual vulnerability. At each level of extinction,

the percentage of remaining microbial diversity was compared to the one obtained from a random loss of the same number of scleractinian corals and fishes, computed 100 times. Deviation from this random loss was assessed by computing a P-value, calculated as the rank of the mean diversity value in the 100 replicates of the extinction scenario, among the increasingly sorted diversity values of all 100 replicates of the random scenario. We considered that the deviation from the random scenario was significant when $P<0.05$, meaning that the diversity value in the observed community was lower than the 5% lowest diversity values following the random loss of animal taxa.

RESULTS AND DISCUSSION

High diversity of animal microbiomes

In our entire dataset made of 74 animal taxa and 35 samples of plankton, prokaryotic diversity hosted by animal surfaces contributed to 95% of total phylogenetic richness (Faith's PD) on rarefied data (Figure 1a and b; un-rarefied data in SM2-1). Individual fish and *Anthozoa* samples contained slightly more ASVs than 200-mL planktonic samples (SM2-2). A recent study found on average 5 times more 97%-identity bacterial Operational Taxonomic Units (OTUs) in 1L of seawater than in coral mucus [36]. Such different results may be due to the contrasting volume of coral microbiome vs. seawater compared, a coral surface of 15-20 cm^2 (see SM1-5) to 0.2 L water samples in our study vs. ~2cm^2 to 1L of seawater in this former study. Similarly, differences in the protocols used (*i.e.* biomolecular methods and data analysis pipelines) may explain such discrepancies.

Average surface microbiome recovered from each animal taxon (fish species, coral genus, or other invertebrate taxon) was phylogenetically richer and more diverse than a 200-mL water sample (KW on Faith's PD and Allen's index on rarefied and un-rarefied data, $P<0.001$), with one animal taxon hosting on average 4.9±2.4% of the total branch length of the phylogenetic tree grouping all ASVs recovered in the rarefied dataset, while one 200-mL water sample contained on average only 1.7±0.2% of the total branch length (Figure 1c and d; un-rarefied data in SM2-1). Additionally, 35 randomly chosen average animal microbiomes reached ca. 8-fold higher phylogenetic richness than our 35 water samples (Figure 1a), indicating that at a similar sampling effort, animal taxa host higher prokaryotic diversity compared to seawater. When considering un-rarefied data, the gap between both types of communities was narrower (SM2-1). Similar results were obtained based on ASV richness (SM2-3).

ASVs unique to animal surfaces (*i.e.* not detected in plankton) made more than 85% of total phylogenetic richness (Figure 1b, un-rarefied data in SM2-1), demonstrating that most of the prokaryotic phylogenetic richness was associated to animal microbiomes. 16.8% of such ASVs were abundant to moderately abundant on animal surfaces, *i.e.* belonging to the top 20% most abundant ASVs (Figure 2; un-rarefied data in SM2-4). By contrast, only 0.3% of the ASVs unique to plankton belonged to the 20% most abundant ASVs in planktonic samples. These results suggest that a significant portion of animal microbiome is specialized to host-associated lifestyle and may not thrive in the water column, while the most abundant planktonic prokaryotes were also capable to colonize animal skin. Such transient colonization of animal surface microbiomes may be a result of water contamination [37], or may permit host adaptation to environmental fluctuations [38].

Bacterial composition

Bacteria dominated communities, accounting for 99.1±1.8% of sequences. The 18 dominant bacterial classes in animal microbiome are depicted in Figure 3a. 72% of them were also detected among the dominant classes in the whole microbiome of corals [39–41], and 61% and 50% were also detected on temperate fish skin and on tropical fish gills, respectively [42,43]. Two classes, *Gracilibacteria* and *Campylobacteria,* were not reported to be associated to animals in the aforementioned studies. *Gracilibacteria* belongs to the Candidate Phyla Radiation (CPR), containing ultra-small bacteria that are recovered from diverse environments and have a probable symbiotic lifestyle [44]. *Campylobacteria* contained mostly the genus *Arcobacter* in our study (up to 8% of abundance). This genus usually inhabits the human or animal gastrointestinal system, though free-living strains have been isolated in various environments [45]. This genus has been isolated from coral disease lesions [46,47]. It has also been recovered from corals exposed to fish farm effluents and in thermally-stressed corals [48,49]. Here, while the corals were apparently healthy and sampled far from coastal cities (SM1-1), the high temperatures at the time of sampling (SM1-2), together with a potential contamination of the lagoon by human faeces due to the absence of effluent treatment in Mayotte [50] may explain the presence of this genus.

Structure of prokaryotic communities recovered on animal surfaces was significantly distinct from plankton (PERMANOVA on W-Unifrac on rarefied data, P=0.001, R^2=0.29, Figure 3a, b and c, un-rarefied data and U-Unifrac in SM2-5 and 6). Plankton was mostly enriched in *Alphaproteobacteria* (especially SAR11 and SAR86 clades), *Cyanobacteria* (especially

Prochlorochoccus and Synechococcus), and the actinobacterial family *Actinomarinaceae* (Figures 3a and SM2-6 and 7). All these clades are abundant and widely distributed marine photoautotrophs and photoheterotrophs displaying small cell sizes and genomic reduction [51–55], that may be selected by the very oligotrophic conditions of surface ocean [56]. The presence of such taxa on our sites suggests that the reefs were well preserved from coastal eutrophication at the time of sampling.

By contrast, animal surfaces were mostly enriched in *Gammaproteobacteria* (especially *Endozoicomonas*), *Firmicutes* (especially *Clostridia*), *Betaproteobacteriales* (especially *Burkholderiaceae*), the alpha-proteobacterial *Rhizobiales* and *Sphingomonadaceae,* and *Verrucomicrobia.* Such clades have been previously identified in temperate and tropical marine fish skin, gut and gill microbiomes [42,43,57–61], and at the surface or inside marine invertebrates [9,58,62,63]. *Endozoicomonas*, especially, is associated to a wide range of hosts, from fish to hard and soft corals, sponges and tunicates, and is hypothesized to play a significant role in host's nutrition and health [58]. Particularly, *Endozoicomonas* genomes show enrichment in several functions that may help to cooperate with various types of hosts (e.g. protein secretion and carbohydrate transport), but also potential functional specialization depending on their hosts [64], that might explain the ubiquity of such genus on the wide diversity of animals studied here. To confirm this hypothesis, such taxonomic assessment of animal-associated microbiomes should be completed by studies assessing the functions that are necessary for bacteria to thrive on marine hosts.

High dissimilarity between animal microbiomes

The high phylogenetic diversity of animal surface microbiomes was paired with a 2.3 times higher variability among those microbiomes than among planktonic samples (PERMDISP on W-Unifrac on rarefied data, $P<0.001$, Figure 3c and SM2-5). The three major animal groups sampled, *i.e.* teleostean fishes, *Anthozoa* and other invertebrates, hosted significantly different prokaryotic communities at their surface, with the distinction between such groups explaining between 5% and 11% of variability (PERMANOVAs, $P<0.001$, SM2-8). However no significant biomarker was identified using LEfSe analysis for each of these groups, indicating that there is no consistently enriched bacterial clade in all animal taxa of these groups, as highlighted by the high dissimilarity between taxa within each group (Figure 3b and c, SM2-5).

Among each main animal group, there was a significant effect of animal taxon on surface-associated microbiome structure and composition (PERMANOVAs, SM2-8). Interestingly, while the larger animal groups explained up to 11% of microbiome dissimilarity, the effect of such smaller taxa explained from 34% (for coral genera) to 49% (for fish species) of surface microbiome variability (PERMANOVAs on rarefied data, P<0.001; SM2-8).
While the species-specificity of marine animal skin microbiome has already been reported [7], here we report that this interspecific variability within a clade is as high as between different clades that diverged ~800 Mya (Figures 3c and SM2-5, divergence time estimate between *Teleostei* and *Anthozoa* according to http://www.timetree.org/). This finding suggests that the correlation between host phylogenetic relationships and microbiome composition, a pattern called 'phylosymbiosis', that has been evidenced in numerous animal models including microbiomes of tropical fish skin, sponges and coral skeleton [7,36,65], may be unobservable at deeper phylogenetic level due to the very large phenotypic differences between the hosts that would saturate this signal.

Exceptional reef microbial diversity

As a consequence of the coupled high diversity and high variability of animal surface microbiomes, the prokaryotic diversity sampled on animal surface microbiomes in this study is far from reaching an asymptote (Figures 1a, SM2-1, SM2-3). We estimated that the total sampled and un-sampled bacterial diversity associated to the subset of reef animals we sampled would range from 8,700 to more than 20,000 97%-identity bacterial OTUs, respectively on rarefied and un-rarefied data (SM2-9).
Recent estimate of world's bacterial diversity predicted that there exists 0.8–1.6 million prokaryotic OTUs worldwide [66]. Our richness estimates correspond to 0.5% to 2.5% of such global diversity. This is striking, given that coral reefs occupy less than 0.1% of surface worldwide, with southwestern Indian Ocean coral reefs making 1.8% of that surface (0.001% of global surface, www.reefbase.org/). Here, we based our estimates on carefully curated ASVs grouped as 97%-identity OTUs, which prevented any overestimation of prokaryotic richness at a local scale [67]. In addition, we only sampled a <7% subset of animal diversity in Mayotte's lagoon, hosting more than 700 fish species [68], 57 soft corals [69], 22 sea cucumbers [70], more than 200 scleractinian species and subspecies, 13 *Asteroideae*, 36 ascidians, 56 bivalves and 23 *Ophiuroideae* [71]. We also did not sample any species from other phylogenetically contrasted clades such as sharks and rays, sea turtle and mammal,, and vegetal species inhabiting Mayotte's lagoon. Likewise, we did not sample the microbes living

within the tissue and skeleton of corals nor those living in fish guts. Our claim is that coral reef communities, just as they host a large portion of marine macrobial diversity compared to their surface [1], may also support a significant proportion of global marine prokaryotic diversity. More extensive sampling on the thousands of coral reef animals on different coral reefs will allow refining the estimates provided here.

Vulnerability of reef microbial diversity

The loss of an animal species due to environmental disturbances at a given location induces the loss of its associated unique microbial diversity. We classified fish species and scleratinian genera depending on their respective vulnerability, to the combined overfishing and habitat loss in the case of fish, and ocean warming in the case of corals (see **Methods** and SM1-7). There was no correlation between animal vulnerability and microbial diversity at its surface (Spearman correlation tests, $P>0.05$). Microbial diversity erosion following macroscopic extinction scenarios revealed that the loss of the 50% most vulnerable coral and fish species for which we had vulnerability data would induce a loss of ca. 28 to 29% of ASVs (SM2-10) and 23% of phylogenetic richness (Figure 4a and SM2-11). Such lower phylogenetic erosion indicates a moderate phylogenetic redundancy between animal surface-associated ASVs. The slope of microbial diversity extinction was only slightly steeper with increasing loss of macroscopic species (Figure 4b and SM2-11). Accordingly, levels of prokaryotic diversity loss were not significantly different from that expected under a random extinction scenario, because the most vulnerable animal species and less vulnerable ones host partially redundant prokaryotic diversity.

To our knowledge, no quantified vulnerability measures exist for invertebrates other than sessile *Anthozoa*, so we did not include them in our extinction scenario. In our dataset, microbiomes of invertebrates other than *Anthozoa* showed the highest diversity and variability (Figure 3c, SM2-2, SM2-5), suggesting that the loss of such warming-sensitive taxa [72], as well as those targeted by humans [73], would induce a more severe erosion of coral reef microbial diversity than the one simulated here. Our results should be further completed by an assessment of the functional erosion that may result from anthropic activities, as such unique phylogenetic diversity in animal microbiomes may also host unique microbial functions in coral reef ecosystems [74]. Finally, our scenario did not account for potential direct effects of anthropic stressors (warming, acidification) that could alter the diversity and functions of microbiomes [75].

CONCLUSIONS

Reef animals macro-organisms host a high and unique diversity of microbes at their surface. Hence, the thousands species living in coral reef ecosystems may support a substantial part of marine microbial diversity. For now, roles of animal surface microbiomes for ecosystem functioning are only partially described, but could be essential (*e.g.* production and degradation of dimethylsulfoniopropionate, a crucial molecule in sulphur cycling; [4]). Future studies should investigate to which extent these unique and vulnerable microbial lineages present on animals contribute to coral reef functioning and possible consequence of their loss in the Anthropocene.

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Data accessibility

Sequence data is available in the NCBI Sequence Read Archive database under the biosample numbers SRS2702344-SRS2702519 and SRS4077375-SRS4077501. Bacterial ASV table and associated metadata and sequences are available on DRYAD repository (https://doi.org/10.5061/dryad.wh70rxwjw).

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Competing interests

The authors declare that they have no competing interests.

Authors' contribution

MC, TB and SV contributed to the conceptualization of the study. MC, CB, NAJG, TB, and SV contributed to the methodology. MC, J-CA, CB, TC, CXRO, FR, ES, and SV helped in the investigation. MC conducted the analyses and writing of the original draft. MC, J-CA, YB, CB, TC, NAJG, FR, ES, TB, and SV contributed to writing, reviewing, and editing of the manuscript. TB, MC and SV helped in the acquisition of funding. TB and SV supervised the study. All authors read and approved the final manuscript.

FIGURES

Figure 1. Phylogenetic diversity of reef microbial communities

(a) Accumulation curves showing the phylogenetic richness (Faith's PD, expressed in percentage of maximum PD of the entire dataset) obtained from animal surface microbiomes and planktonic communities, depending on the number of randomly selected planktonic communities or animal taxa, represented as the mean ± the standard deviation across 100 random subsamples. (b) Venn diagram representing the percentage of phylogenetic richness unique to animal surface microbiomes after pooling all animal taxa and to planktonic communities, and shared between both compartments. (c and d) Boxplots of (c) Percentage of PD and (d) phylogenetic diversity (Allen's index) recovered from animal surface microbiomes and plankton. The same figure based on un-rarefied data is provided in SM2-1. Accumulation curves and Venn diagram based on ASV-richness are provided in SM2-3.

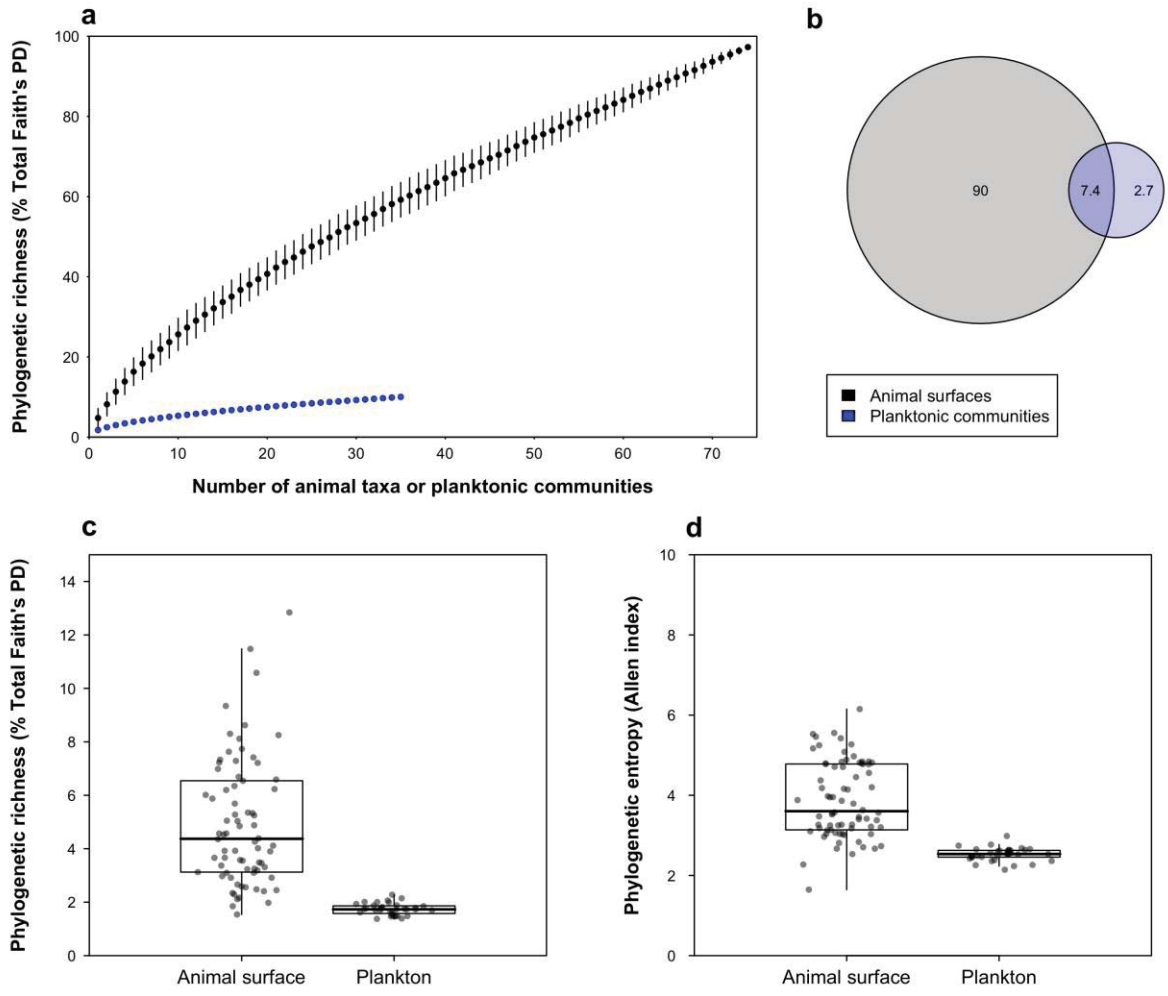


Figure 2. Abundance of ASVs in animal surface microbiomes and plankton.
(a and b) Average rank-abundance curves obtained from surface microbiomes of (a) animal surface microbiomes and (b) planktonic communities. Vertical dotted lines represent 5, 10, 20 and 50% threshold for most abundant ASVs. The average evenness of ASVs abundances (Bulla's *O*) in each compartment is indicated on the corresponding plot. (c) Rank of abundances of ASVs unique to animal surface microbiomes or to plankton within respective microbial communities. The same figure based on un-rarefied data is provided in SM2-4.

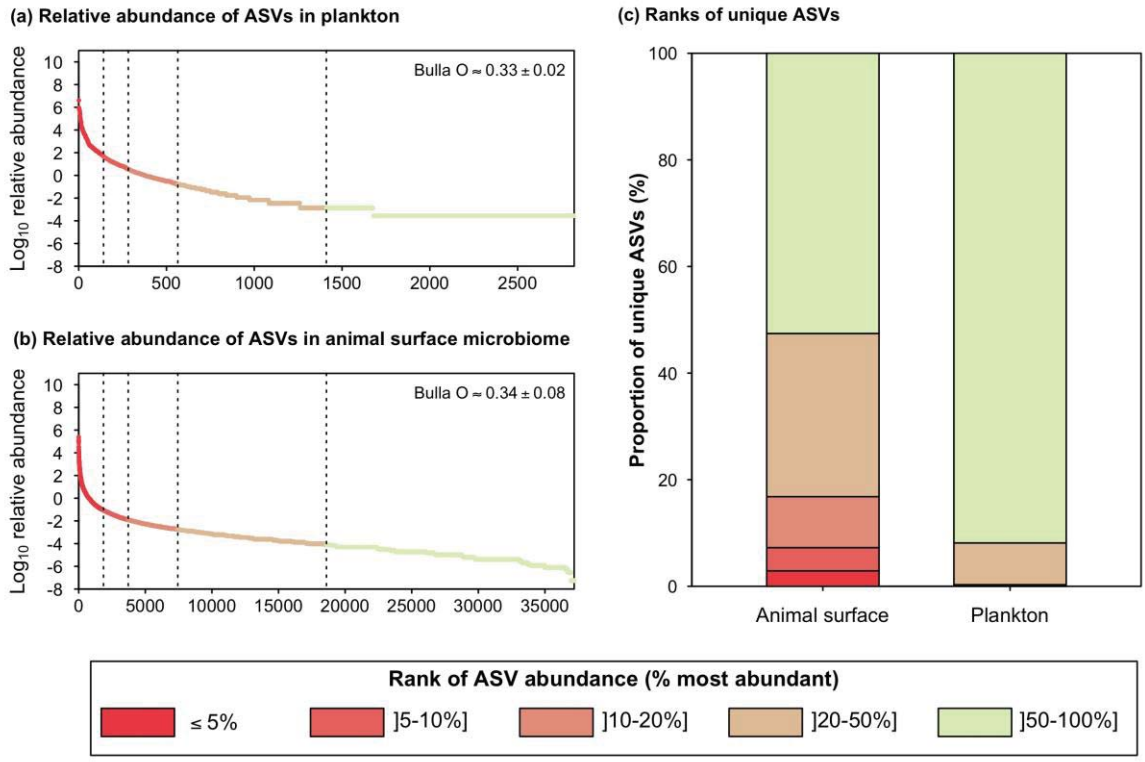


Figure 3. Dissimilarity in taxonomic and phylogenetic structure of microbial communities from plankton or animal surfaces

(a) Dominance of 18 prokaryotic classes for animal surface microbiomes (averaged by fish families, *Anthozoa* genera and other invertebrates' taxa) and for plankton (averaged across all 35 planktonic communities). (b) Microbial communities are plotted on the two first axes of a PCoA computed on W-Unifrac. (c) Intra-and inter-group W-Unifrac. Results based on un-rarefied data and on U-Unifrac are provided in SM2-5 and 6.

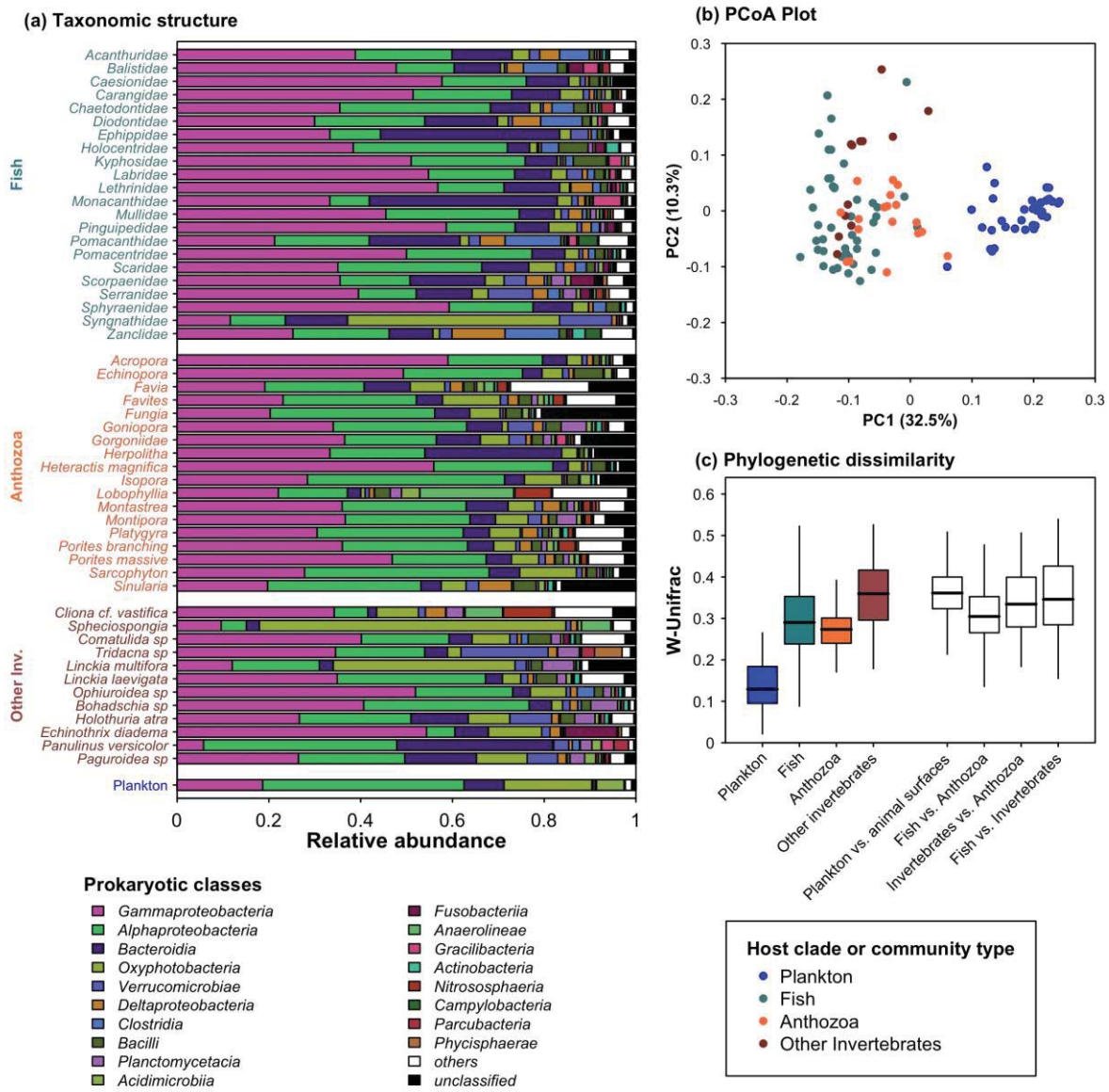
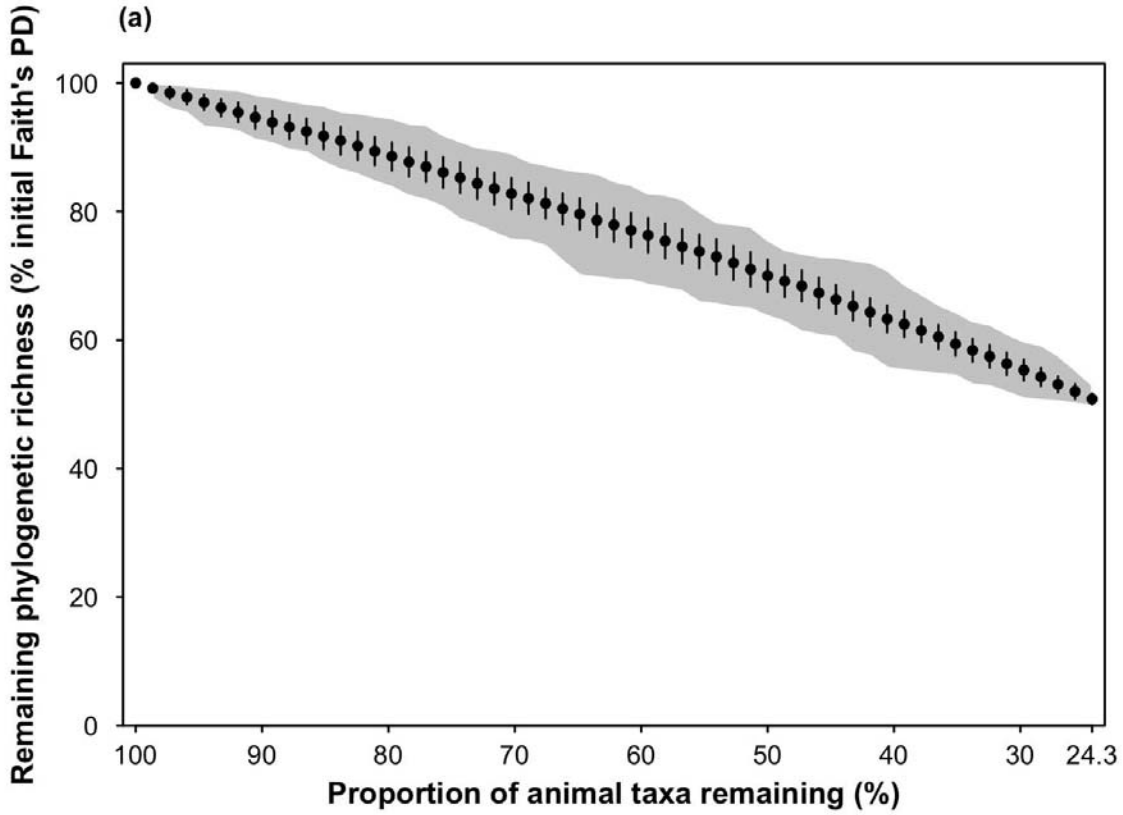
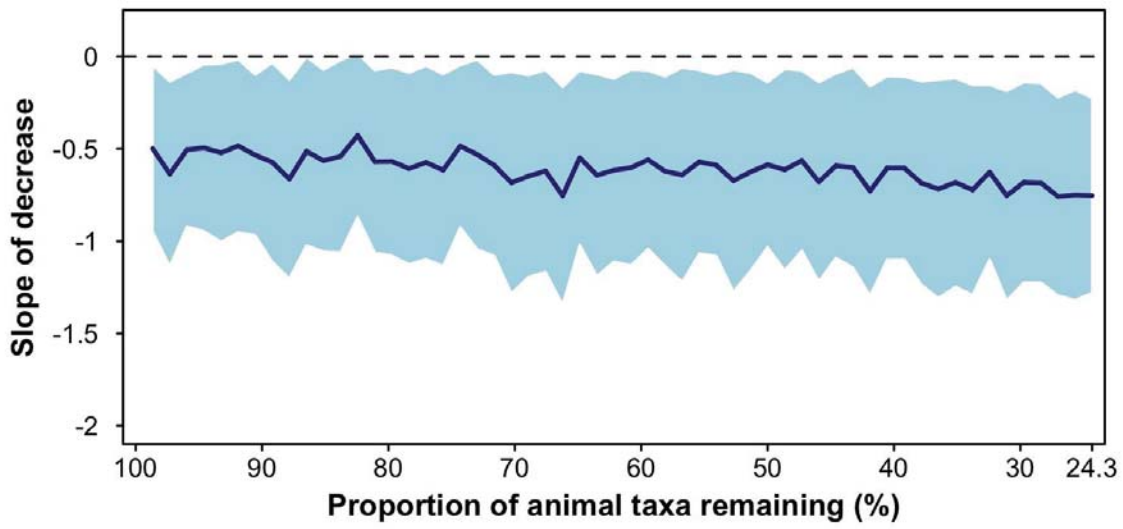


Figure 4. Vulnerability of coral reef microbial phylogenetic richness to loss of fishes and scleratinian corals.

(a) Mean (±SD) of remaining prokaryotic phylogenetic richness on the studied coral reef for a given proportion of animal taxa lost according to the simulated erosion scenario (100 replicates). When 100% of coral and fish species included in the scenario are lost, the remaining microbial phylogenetic richness corresponds to the one of prokaryotic communities associated to plankton and animal taxa that were not included in the extinction scenario (*i.e.* 24% of taxa, corresponding to *Isopora*, soft corals, gorgonians, anemone and all non-anthozoan invertebrates). Scenario simulating a random loss of fishes and corals (*i.e.* species removed independently from their vulnerability) is illustrated with the grey area representing the range of remaining phylogenetic richness among 100 replicates.

(b) Mean (solid line) ± SD (shaded area) of slopes of phylogenetic richness loss calculated at each level of extinction on all 100 replicates. The same analyses based on un-rarefied data and on ASV richness are provided in SM2-10 and 11.


(a)
Remaining phylogenetic richness (% initial Faith's PD)
100
80
60
40
20
0
100
90
80
70
60
50
40
30
24.3
Proportion of animal taxa remaining (%)


Slope of decrease
0
-0.5
-1
-1.5
-2
100
90
80
70
60
50
40
30
24.3
Proportion of animal taxa remaining (%)