1 **Title:** Functional Redundancy in Ocean Microbiomes Controls Trait Stability

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Abstract:

Theory predicts that functional redundancy in microbial communities increases trait stability, meaning that traits or functions are less likely to be lost from the community when species go extinct. However, few experiments have empirically tested this prediction, especially in the context of microbial communities and at the landscape scale. In part, the lack of metrics for functional redundancy in microbial ecosystems has prevented addressing this question. In a companion manuscript we proposed a quantitative metric for functional redundancy called Contribution Evenness (CE) that is optimized to reflect trait stability. Here, we use CE to predict the stability of marine microbial functions to species and transcription loss. Using transcriptomes deposited in the Ocean Microbial Reference Gene Catalog (OM-RGC.v2), a catalog of genes and transcripts sequenced by the TARA Ocean expedition, we quantified the functional redundancy for 4,314 KEGG Orthologs (KOs) across 124 marine sites. Functional redundancy was highly correlated with a latent variable consisting of four ocean physiochemical parameters: oxygen and chlorophyll a concentrations, depth, and salinity. Functional redundancy was higher at the poles than in non-polar regions. Simultaneously, regional β-diversity for individual functions was higher for functions with higher functional redundancy. These observations provide evidence that higher functional redundancy indicates increased stability of microbial ecosystem functions on spatiotemporal scales consistent with surface ocean mixing. We suggest that future changes in ocean physiochemistry could likely influence this stability for functions with lower functional redundancy.

Importance

Functional redundancy describes the state of multiple species performing the same function. Theory suggests functional redundancy stabilizes microbial community functions from disturbances leading to species loss or other changes to the microbiome. Previous work suggests that functional redundancy is common in ocean microbiomes which implies traits should be more stable among metacommunities. Some laboratory experiments demonstrate this idea, but it is difficult to test in the natural world. In a companion manuscript, we proposed a functional redundancy metric sensitive to trait stability. Here, we used this metric to show that functional redundancy varied substantially among ocean microbiomes and that regions with higher functional redundancy had higher regional trait stability. Last, we noted that variations in functional redundancy strongly correlated to ocean physiochemistry. Thus, changes in ocean physiochemistry via climate change may alter community traits to become more or less resistant to disturbance relative to contemporary conditions.

Introduction

The ability to resolve complete genomes in microbial communities via contig binning and single-cell genome sequencing has revealed that metabolic functions, or traits, are often present in multiple taxa within a microbiome (1–4). The practical consequences of functional redundancy, in terms of community composition and function, are not well understood for microbial communities. Theoretical predictions, developed in the context of macroecosystems, suggest that functional redundancy can buffer a community against function loss due to species extinction (5–9). Foundational work on grassland ecosystems validated these theoretical predictions by showing that plant community biomass stability increased with higher functional redundancy (10). Mesocosm experiments provide empirical evidence that functional redundancy may also buffer microbial ecosystem functions from species loss. For instance, microbial density and biomass was less variable for assemblages with redundant populations occupying different trophic guilds in a food web (11), and reduction-oxidation conditions in sediment communities were more stable with higher bacterial diversity and niche overlap (12). Although existing theoretical and empirical evidence suggests functional redundancy may enhance ecosystem function stability, small-scale and mesocosm experiments with microbial communities may not reflect the most important processes on ecosystem scales (13). Establishing whether functional redundancy stabilizes traits is important for understanding how environmental fluctuations, most notably climate change, may influence microbially-mediated biogeochemical cycles.

In a companion paper, we developed a metric for functional redundancy called contribution evenness (CE) (14). CE uses genes or transcripts as traits (15, 16) and measures how evenly taxa contribute to the community-wide level of these traits (total gene abundance in the case of genes, and total transcript abundance in the case of transcripts). CE is optimized to

reflect how stable microbially-catalyzed functions are to random species extinction or transcription loss in communities. Here, we use CE to address three fundamental questions about functional redundancy in marine microbial metacommunities:

1.) Does functional redundancy of ocean microbiomes vary geographically,

2.) If so, does this variation relate to the physicochemical environment, and

3.) What ecological consequences are apparent from observed patterns in functional redundancy?

To answer these questions, we used KEGG orthology (KO) annotations of genes reported from 180 sites sampled during the TARA Oceans expeditions, plus transcripts reported from a subset of 124 of those sites (17). KEGG is an attractive ontology because the functions of KOs are biochemically well-characterized and provide a reasonably large coverage of predicted genes in marine microbiomes. The *TARA Oceans* dataset is ideal for this work because it encompasses a diverse set of sites and marine ecosystems, which were sampled with generally standardized methods (18). By applying CE to the *TARA Oceans* data set, we identified geographic variations in functional redundancy, identified physicochemical factors relating to this variation, and established that microbial functions were less stable in regions with lower functional redundancy. These observations combined allowed us to identify some possible effects that climate change may have on the resilience of microbial community function to local disturbance.

Methods

TARA Oceans Genes and Environmental Data

We downloaded the entire Ocean Microbial Reference Gene Catalog v2 (OM-GRC.v2) on 1 Feb 2021 from EMBL-EBI (BioStudy: S-BSST297) and the environmental data from https://doi.org/10.5281/zenodo.3473199 (17). This data set includes annotations and abundance

for metagenomes from 180 unique sites and transcriptomes from 124 sites. Gene and transcript profiles correspond to biological sequences collected from 100L of seawater on filters with size ranges 0.22-1.6 μm or 0.22-3.0 μm (18). Analysis was limited to sequences in OM-RGC.v2 annotated to KEGG orthologs (KO) (19). We interpreted length-normalized short-read mapping frequencies as abundances. These values are reflect the abundance of any sequence in a metagenome or transcriptome, given a fixed sequencing effort. Gene abundances for KO single copy marker genes (list below) annotated to the same genus were averaged to estimate the abundance of a given genus. Our selection of genus level analysis was to mitigate noise associated with analyzing functional redundancy of ASVs, which is theoretically possible. To allow for meaningful comparisons of functional redundancy at different sites, we rarified sequencing effort at each site. Relative abundances were then used as weights during random sampling, with replacement. Each site was sampled 3358334 and 472163 times for gene and transcript profiles, respectively. These values corresponded to the lowest sampling effort among all metagenomes and transcriptomes, respectively.

KO Functional Redundancy and Diversity

Functional redundancy was calculated for each KO at each site for both metagenomes and metatranscriptomes. Functional redundancy was calculated with Contribution Evenness (CE) as detailed in the companion paper (14). Here, we treat KOs as proxies for metabolic traits (16, 20). In brief, the abundance of sequences sharing the same KO annotation in a sample was summed together, without regard to genus. Subsequently, the abundance of genes for individual genera was normalized by the summed abundance to obtain a relative abundance of each gene, for each genus. This vector corresponds to the relative contribution distribution (equation 3.2 in the companion paper). Species richness (S) used for calculating CE in equation 8 in companion

paper was calculated with KO single copy marker genes. The presence of a genus was determined by summing the abundance of single copy marker genes: K06942, K01889, K01887, K01875, K01883, K01869, K01873, K01409, K03106, and K03110. If the summed abundance was greater than 0, then the genus was considered present in the metagenome/metatranscriptome.

Global Modeling of Functional Redundancy

We sought to characterize spatial trends in the functional structure of microbial communities. To do this, we performed redundancy analysis using the rda function from the R package, vegan (21). In this analysis, the functional structure of microbial communities was treated as a response variable and physio-chemical variables were treated as predictor variables. For sites where a given KO was absent, the KO was assigned a value of zero. This situation occurred ~13.6% and 18.5% of the time for gene and transcript profiles, respectively. Low functional redundancy does not necessarily imply that a function is ecologically unimportant. This is particularly true for traits with low functional redundancy that strongly correlate to phylogeny. Such examples include *Thaumarchaeota* and diazotrophs which act as the primary nitrifiers and nitrogen fixers in the ocean, respectively (22). On the contrary, small changes in functional redundancy for traits with low functional redundancy might reflect key ecological processes, and thus, comparisons of community functional structure should account for the differences in functional redundancy magnitude. Thus, changes in KO functional redundancy reflected changes with respect to the KO's observed variance while not reflecting the KO's order of magnitude, which spanned five orders of magnitude. To prevent functions with large CE from dominating the redundancy analysis, we normalized CE for each KO at each site by the respective KO's variance from across all sites. For the redundancy analysis, we used salinity (PSU), nitrate (mmol m^{-3}), phosphate (mmol m^{-3}), oxygen (mmol m^{-3}), chlorophyll A (mg m^{-3}),

130 depth (m), and silicate (mmol m^{-3}). We chose these variables as they were *in situ* measurements
131 (18) and could scale with models that predict global ocean chemistry. We imputed missing data,
132 as removing incomplete cases can bias datasets (23). Random forest imputation was performed
133 using the missForest function, from the R package, missForest (24). Next, each environmental
134 variable was converted into a normal distribution using a boxcox transformation via the boxcox
135 function in the R package, MASS (25). Variables were then centered to have a mean of zero.
136 Last, the significance of each variable as well as the first two canonical axes was verified using
137 the anova.cca function in the R Package, vegan (21).

138 The first canonical axis derived from the redundancy analysis was used to predict mean
139 transcript functional redundancy from the individual metatranscriptomes (sites) using OLS
140 regression. This model was compared to an OLS regression using salinity, nitrate, phosphate,
141 oxygen, chlorophyll A, depth, and silicate as predictors of mean transcript functional
142 redundancy. Similar to before, missing data were imputed using missForest (24), variables were
143 transformed with a boxcox transformation (25), and variables centered so the mean distribution
144 was zero prior to regression. The best predictor subset was determined using the regsubsets
145 function from the R package, leaps (26). The criteria defining the best model was minimizing
146 AIC.

147 The monthly-averaged data products spanning from Jan 2013 to Dec 2018 for
148 GLOBAL_REANALYSIS_BIO_001_029 and GLOBAL_REANALYSIS_PHY_001_031 were
149 downloaded from https://marine.copernicus.eu/ on 7 May 2021. Data products had a grid
150 resolution of 0.25°x0.25°. The OLS regression using the first canonical axis as a predictor
151 substantially outperformed the best subset OLS when predicting mean transcript functional
152 redundancy. We therefore converted the predicted data product chemistry for each grid cell into

a score for the first canonical axis. Then, the mean transcript functional redundancy was predicted for each grid cell, for each month, utilizing the coefficient derived from the canonical axis OLS regression. The median, 5^{th} percentile, and 95^{th} percentile of mean functional redundancy was taken across the six-year window. Variance was measured as the difference between the 95^{th} and 5^{th} percentile divided by the median.

Metatranscriptome β-diversity and Trait Stability

The *β*-diversity (27) was calculated for individual functions (KO) across different regions. Regions were defined as a metatranscriptome and the nine closest metatransciptomes in the epipelagic (depth < 200m). Site distances were measured using the published site coordinates (17) and the *distm* (default parameters) function from the R package, geosphere (28). Redundant combinations of sites were removed prior to reporting results. The average functional redundancy for individual functions was taken for each region. The *β*-diversity was calculated as:

$$D(H_\beta) = \frac{D(H_\gamma)}{D(H_\alpha)} \quad (2$$

Here, we used a diversity order q=0, or the richness to calculate diversity. As such, *γ*-diversity was either 0 (regionally absent) or 1 (regionally present), and *α*-diversity was the proportion of local communities with the trait. Since *β*-diversity is not defined for traits completely absent from a region, the *β*-diversity calculation simplified to:

$$D(H_\beta) = \frac{1}{f} \quad (3$$

which is simply the inverse proportion (*f*) of local communities in a region with a given function.

Results and Discussion

We used CE (14) to measure functional redundancy for KEGG ortholog (KO)-annotated genes from 180 and 124 *TARA Oceans* metagenomes and metatranscriptomes, respectively (17). CE uses genes (CE with respect to genes) or transcripts (CE respect to transcripts) as traits (15, 16) and measures how evenly species in a community contribute to these traits as a whole. After calculating CE for metagenomes (Fig. 1A) and metatranscriptomes (Fig. 1B), we found that KOs spanned over three orders of magnitude, demonstrating the high degree of variability in how functionally redundant traits are in the ocean. We further isolated KOs based on KEGG energy metabolism classification to illustrate how functional redundancy varied across the ocean for sulfur, photosynthesis, oxidative phosphorylation, nitrogen, methane, and carbon fixation. The distribution of transcript abundance within ocean microbiomes correlated well with the distribution of gene abundance at the same site (Fig. 1C; R^2=0.45, $p<0.001$). This relationship was not surprising considering previous reports that metagenome gene abundances strongly influenced transcript abundances across *TARA Oceans* microbiomes (17). Although the nature of these observations is similar, the ecological implication is different. Specifically, the observation of Salazar et al. shows correlation in absolute gene abundance and transcription abundance, whereas our observation indicates that when genomic traits are more evenly distributed across genus within a community, transcription is also more evenly distributed across genus.

To better understand the relationship between environmental characteristics and functional redundancy, we used redundancy analysis (RDA) to model the functional redundancy of each KO at each site as a function of the seven environmental parameters: salinity, depth, and concentrations of nitrate, phosphate, and silicate ions, oxygen, and chlorophyll a (Fig. 1). The first canonical axis of this model explained 19.8% of the total functional redundancy variance in 4,314 transcripts annotated as KOs. An ANOVA demonstrated that the first canonical axis

196 explained significantly more variability in KO functional redundancy than a null model (p<0.01)
197 (29). Although the total explanatory power for individual KOs was low, we found that the
198 average functional redundancy of all KOs at each TARA Oceans site was accurately predicted by
199 the first canonical axis alone (93.2% of total variance explained; ordinary least squares
200 regression.

201 Factor loadings of this first canonical axis were dominated positively by oxygen and
202 chlorophyll a and negatively by sample depth and salinity (Fig. 2B). Thus, this canonical axis
203 appears to be a proxy for phototroph biomass, or the extent to which an environment is
204 dominated by copiotrophs versus oligotrophs. The strong predictive power of chlorophyll a was
205 not surprising given that carbon export mediated by primary productivity is known to be a good
206 predictor for community composition and genomic composition in the ocean (30). Higher
207 functional redundancy was positively correlated with this proxy for phototroph biomass. We
208 compared the performance of our factor-based model to a best subset (based on an AIC criteria)
209 OLS regression using the original seven physiochemical variables (NO_3^-, PO_4^{3-}, salinity, depth,
210 O_2, Si, and ChlA) that generated our factor (Fig. 2C). In contrast to the factor model, the best
211 subset model (O_2, Si, and depth) explained only 32.4% of the variance in mean functional
212 redundancy.

213 The high explanatory power by the environmental data justified extrapolating our factor
214 model onto a global scale. Using global predictions of ocean nutrient concentrations, we
215 calculated factor scores at a 0.25°x0.25° resolution and predicted functional redundancy across
216 Earth's oceans using the derived coefficient from our OLS regression of mean functional
217 redundancy versus the first canonical axis of the RDA. Our model predicts that functional
218 redundancy is highest in polar regions and near river outflows, and lowest in subtropical gyres

(Fig. 3A). Variance was highest in polar regions, coastal regions, and river outflows (Fig. 3B). The transition from high to low functional redundancy between polar and non-polar latitudes was consistent with previously reported ecological boundaries for ocean microbiomes, where the transition from non-polar to polar latitudes corresponded to compositional changes in metatranscriptomes and metagenomes (17).

Functional Redundancy as an Indicator of Trait Stability

In the companion paper, we presented a numerical simulation demonstrating a relationship between CE and trait stability to random extinctions. Here, we sought to establish whether there is empirical evidence that functional redundancy increases trait stability in ocean microbiomes, as previously hypothesized (31). Specifically, we hypothesized that if higher levels of functional redundancy do indeed increase trait stability, then the sets of functions present in nearby communities should be more similar when functional redundancy is higher. To test this hypothesis, we compared functional redundancy at each epipelagic site to the β-diversity (27) of each function (coded as present or absent) in a local region consisting of the site in question plus the nine nearest sites. In this context, lower β-diversity indicates that a larger portion of local communities shared a given function (equation 3). Since microbial communities exhibit spatial autocorrelation (32), these ad-hoc local regions serve as a reasonable alternative to the ideal data set, which would consist of subsequent metagenomes taken from a parcel of water over time.

We observed a negative monotonic relationship between functional redundancy and beta diversity for every KO for every unique region (Fig. 4). This qualitative evidence is consistent with the idea that functional redundancy maintains trait stability on a regional level. Notably, CE>0.01 corresponded to functions becoming almost entirely stable within their respective regions (Fig. 4). This threshold suggests a large portion of functions should be stable across

Earth's ocean microbiome (Fig. 3). Nonetheless, select functions do appear vulnerable to regional instability. Notably, nitrogen metabolism functions tend to have CE<0.01 (Fig. 1B). Climate models and historical observations indicate that major ocean currents are slowing (33), oxygen minimum zones are expanding (34), and there will be future changes in regional primary productivity (35). With respect to oxygen and primary productivity, these variables are important in our factor model and suggest that future changes in these parameters might disproportionately influence the stability for lower functional redundancy functions such as nitrogen energy metabolism.

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Competing Interests:

We have no competing interests.

Data and Materials Availability:

The Ocean Microbial Reference Gene Catalog v2 (OM-GRC.v2) is accessible from EMBL-EBI (BioStudy: S-BSST297). *TARA Oceans* site metadata was downloaded from https://doi.org/10.5281/zenodo.3473199. The hindcast data products, GLOBAL_REANALYSIS_BIO_001_029 and GLOBAL_REANALYSIS_PHY_001_031, are accessible from https://marine.copernicus.eu/. All code and processed data is available at https://github.com/taylorroyalty/tara_ocean_fr.

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Figures:

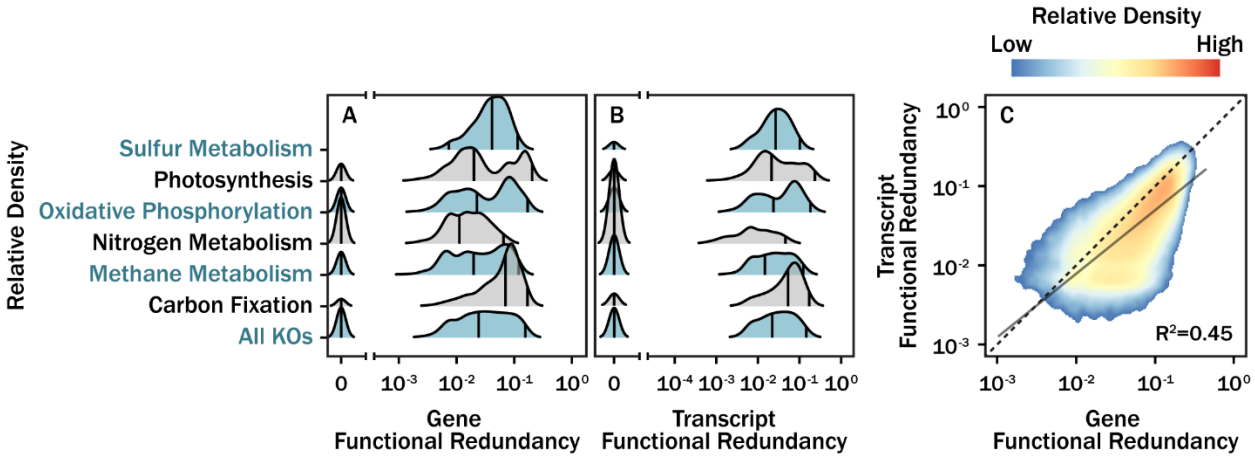
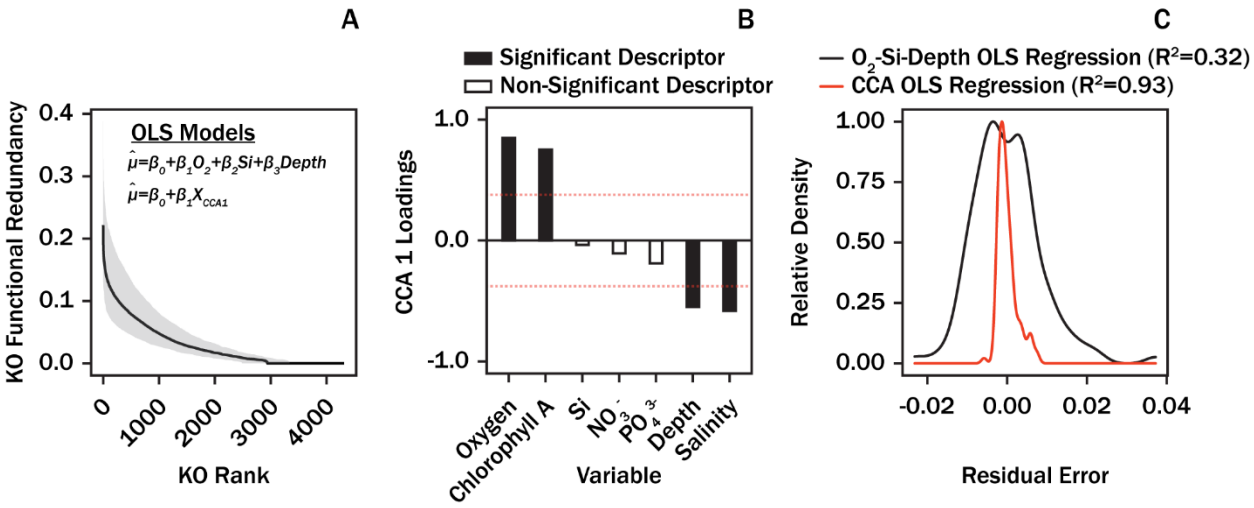


Fig. 1: Variation in functional redundancy for KOs across 180 *TARA Oceans* metagenomes (**A**), 129 *TARA Oceans* transcriptomes (**B**), and a pairwise comparison of functional redundancy ($n \approx 415{,}000$) for KOs annotated the same at the same site (**C**). Density curves (**A,B**) were generated with a kernel density estimate (gaussian kernel with a bandwidth 0.0803). The vertical black lines correspond to 5th, 50th, and 95th quantiles. The metagenomes and metatranscriptomes functional redundancy regression (**C**) followed a $\log_{10}$-$\log_{10}$ model (solid black line). Prior to regression, all values were offset by 10^{-4} and high leverage data was removed based on high Cook's distance ($> \frac{4}{n}$). The color gradient and black dashed line correspond to data density and a one-to-one relationship, respectively.



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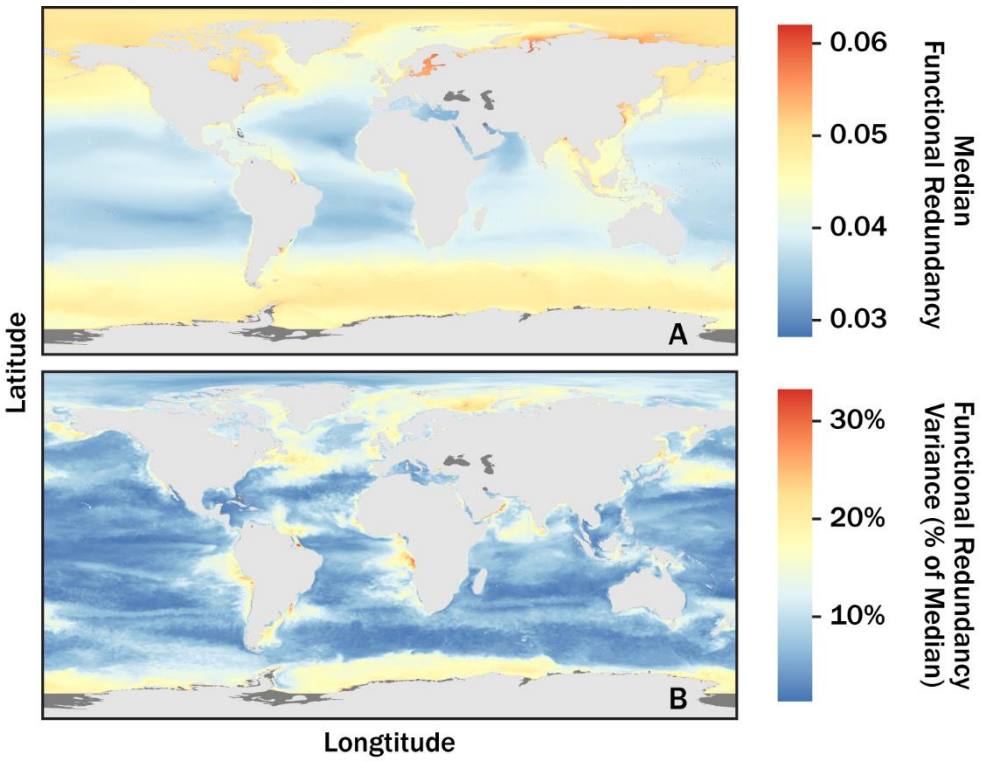
363 **Fig. 2:** Metatranscriptome rank-functional redundancy curves across all *TARA Oceans* sites
364 (n=129) analyzed in this study (**A**). The black line corresponds to the median while the shaded
365 area corresponds to the range spanning between the 5th and 95th percentiles. Proposed models
366 were evaluated for accuracy in predicting mean (μ) and standard deviation (σ) of individual rank-
367 functional redundancy curves. The O_2-Si-Depth model was selected as a best subset (minimum
368 AIC) among the seven predictor variables. Canonical axis 1 loadings (scaling = 0) derived from
369 the redundancy analysis (**B**). Dashed red lines in panel (**B)** correspond to the "equilibrium line of
370 descriptors" ($\sqrt{d/p} = \sqrt{1/7}$), a threshold for defining significant variable contribution to factor
371 loadings (36). A comparison in residual error of mean functional redundancy predicted by the
372 O_2-Si-Depth OLS regression model and the canonical axis OLS regression model (**C**).



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374 **Fig. 3:** Mean functional redundancy of all KOs at a 5m depth across Earth's oceans (0.25° x

375 0.25° resolution). Panels (**A**) and (**B**) correspond to the median and variance of predictions

376 spanning Jan 2013 to Dec 2018, respectively. Dark and light grey correspond to regions absent

377 of predictor data and land, respectively.

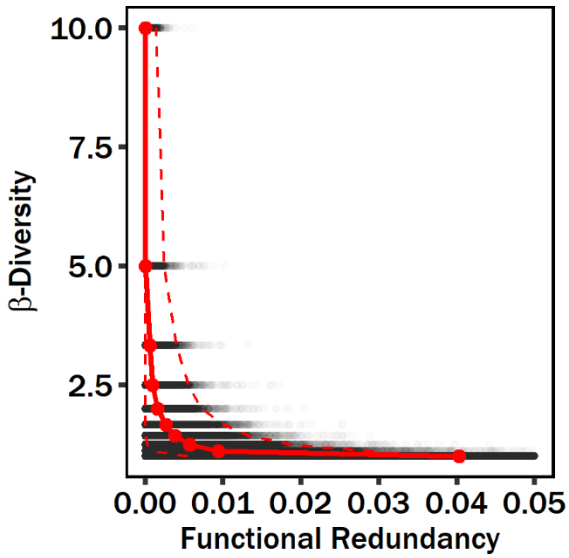

Fig. 4. The β-diversity for individual KOs as a function of the average functional redundancy within local regions. The local region of each site was defined as the site plus the 9 geographically nearest sites. For all regions, the median distance from the region center to sites within the region is 1740 km. The red points and solid red line correspond to the median functional redundancy across all KOs for a given β-diversity. The upper and lower dashed red lines correspond to the 97.5 and 2.5 quantiles, respectively.