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Global Trends in Marine Plankton Diversity across Kingdoms of Life

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1 Global trends in marine plankton diversity 2 across kingdoms of life

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109 **Summary**

110 The ocean is home to myriad small planktonic organisms that underpin the functioning of
111 marine ecosystems. However, their spatial patterns of diversity and the underlying drivers
112 remain poorly known, precluding projections of their responses to global changes. Here, we
113 investigate the latitudinal gradients and global predictors of plankton diversity across archaea,
114 bacteria, eukaryotes and major virus clades using both molecular and imaging data from *Tara*
115 Oceans. We show a decline of diversity for most planktonic groups towards the poles, mainly
116 driven by decreasing ocean temperatures. Projections into the future suggest that severe
117 warming of the surface ocean by the end of the 21st century could lead to tropicalization of
118 the diversity of most planktonic groups in temperate and polar regions. These changes may
119 have multiple consequences for marine ecosystem functioning and services, and are expected
120 to be particularly significant in key areas for carbon sequestration, fisheries, and marine
121 conservation.

122

123 **Keywords**

124 plankton functional groups, macroecology, latitudinal diversity gradient (LDG), temperature,
125 climate warming, *Tara* Oceans, trans-kingdom diversity, high-throughput sequencing, high-

126 throughput imaging

127

128 **Introduction**

129 Our planet is dominated by interconnected oceans that harbor a tremendous diversity of
130 microscopic planktonic organisms. They form complex ecological networks (Lima-Mendez et
131 al., 2015) that sustain major biogeochemical cycles (Falkowski et al., 2008; Field et al., 1998)
132 and provide a wide range of ecosystem services (Guidi et al., 2016; Ptacnik et al., 2008;
133 Worm et al., 2006). The ongoing increase in atmospheric carbon dioxide concentrations is
134 having knock-on effects on the ocean by altering, amongst others, temperature, salinity,
135 circulation, oxygenation and pH (Pachauri et al., 2014; Rhein et al., 2013). These changes
136 have already left visible imprints on marine plankton, fish, mammals and birds, with shifts in
137 species phenology and distribution (Beaugrand et al., 2009; Boyce et al., 2010; Poloczanska et
138 al., 2013; Richardson and Schoeman, 2004). Future increases in ocean temperatures are
139 expected to modify phytoplankton diversity and distribution directly, by altering metabolic
140 rates and growth (Thomas et al., 2012; Toseland et al., 2013), or indirectly through changes in
141 ocean circulation and consequently the supply of nutrients to surface waters (Bopp et al.,
142 2013). Given that such modifications will most likely impair the functions, goods and services
143 provided by the ocean (Brun et al., 2019; Hutchins and Fu, 2017; Worm et al., 2006),
144 predicting how plankton diversity will respond to climate change has become a pressing
145 challenge (Cavicchioli et al., 2019).

146 Unravelling patterns of diversity across macroclimatic gradients, such as the latitudinal
147 gradient of diversity (LDG), is a way to anticipate the impacts of climate change (Algar et al.,
148 2009; Frenne et al., 2013). The LDG, historically studied principally in terrestrial
149 macroorganisms, usually consists of a monotonic poleward decline of local diversity (known
150 as alpha diversity; Whittaker, 1972) for both terrestrial and aquatic organisms (Hillebrand,
151 2004). The LDG is hypothesized to result from a range of non-exclusive ecological and
152 evolutionary mechanisms that operate at multiple spatial and temporal scales (Clarke and
153 Gaston, 2006; Pontarp et al., 2019; reviewed in Willig et al., 2003). Amongst the mechanisms
154 classically invoked, temperature is often thought to be one of the major drivers through two
155 effects. The “physiological tolerance hypothesis” posits that temperature structures the LDG
156 by imposing abiotic constraints on species distribution range (Currie et al., 2004), with fewer
157 species tolerating cold conditions and tropical temperatures being generally below the upper
158 thermal tolerance limit of most organisms. The “kinetic energy hypothesis” relates to the
159 metabolic theory (reviewed in Brown, 2014) which posits that higher temperatures increase
160 the rate of metabolic reactions, resulting in shorter generation times, faster ecological or
161 physiological processes, and ultimately higher mutation and speciation rates, thereby leading
162 to higher local diversity. Beyond temperature, the “productivity/resources hypothesis” posits
163 that greater resource availability and/or primary production in tropical terrestrial areas can
164 support larger population sizes and limit local extinction, thereby promoting species
165 coexistence (reviewed in Clarke and Gaston, 2006). The “environmental stability hypothesis”

166 asserts that short- to long-term environmental instability in extratropical latitudes should
167 cause greater local extinction rates, because life in such unstable environments requires
168 particular and costly physiological adaptations, which would ultimately preclude speciation
169 (Clarke & Gaston 2006). The LDG has also been explained by stronger biotic interactions in
170 the tropics due to higher energy availability, which would increase diversity through
171 complexification and specialization of trophic, mutualistic, or parasitic interactions (reviewed
172 in Willig et al., 2003). However, this hypothesis has found little support in the literature
173 (Hillebrand, 2004), and further relies on the mechanisms exposed above.

174 By contrast, current knowledge about the global trends and drivers of oceanic plankton
175 diversity, ranging from viruses to microbes and zooplankton, remains highly fragmentary. It is
176 mainly based on meta-analyses, which are sensitive to heterogeneous datasets (Brown et al.,
177 2016) and do not systematically capture the diversity of dominant planktonic groups. As such,
178 the form of the LDG remains equivocal for marine bacteria, copepods and diatoms, whose
179 diversity has been reported to either decline linearly poleward (Fuhrman et al., 2008; Righetti
180 et al., 2019; Sul et al., 2013; Woodd-Walker et al., 2002), to peak in extratropical regions
181 (Ladau et al., 2013; Raes et al., 2018; Rombouts et al., 2009), or to adopt weak or inverted
182 latitudinal trends (e.g. Chust et al., 2013; Ghiglione et al., 2012). Viruses LDG have been
183 described only recently, and seem to exhibit an increase of diversity in the Arctic Ocean
184 (Gregory et al., 2019). Consequently, the extent to which the above-mentioned hypotheses
185 apply to the world of marine plankton remains unclear. For example, marine plankton are
186 expected to have huge population sizes, high dispersal abilities, short life cycles and
187 dormancy stages that would prevent local extinctions and reduce speciation rates. The peak of
188 diversity in temperate to high latitudes has also been suggested to support the
189 “productivity/resource hypothesis” (Ladau et al., 2013; Raes et al., 2018), which is in
190 agreement with the oligotrophic status of most tropical waters (Field et al., 1998). On the
191 other hand, the “environmental stability hypothesis” is expected to highly constrain marine
192 plankton at high latitudes, which experience strong seasonality in temperature, nutrients and
193 light, as suggested for phytoplankton (Behrenfeld et al., 2015; Righetti et al., 2019). These
194 constraints may also cascade across trophic levels, as suggested for copepods (e.g. Rombouts
195 et al., 2009). All these uncertainties seriously hamper our ability to understand the drivers of
196 these essential components of marine ecosystems and estimate their potential responses in a
197 changing ocean.

198 Here, we provide a unified view of plankton LDGs using systematically collected data from
199 the *Tara* Oceans global expedition. We combine DNA sequencing of filtered seawater and
200 imaging of net catches to study the diversity in Molecular Operational Taxonomic Units
201 (MOTUs) and morphotype diversity of major groups from all domains of life, as well as both
202 small and large double-stranded DNA viruses (Karsenti et al., 2011). We then examine
203 separately their respective LDGs while determining their best environmental correlates, as
204 they may be influenced by different drivers. Finally, to identify the regions that may
205 experience the most drastic changes in plankton diversity in the future we model the trends of

206 plankton diversity at the global scale for the beginning (years 1996-2005) and end of the
207 century (years 2090-2099; scenario RCP 8.5).

208

209 **Results and discussion**

210 *Latitudinal gradient of diversity across marine plankton groups and water layers*

211 In this study we used a wide collection of uniformly collected data sets with broad latitudinal
212 coverage to explore the local diversity trends of all organismal groups that make up plankton
213 communities (Table S1). Besides already publicly available resources from *Tara* Oceans, we
214 included newly released metabarcoding data of the V9 region of the 18S rRNA gene and flow
215 cytometry abundances both from the Arctic Ocean. We further complemented these
216 observations with new global-scale data sets obtained with amplicon sequencing, microscopy
217 and imaging techniques. Our data sets were derived from 189 sampling stations distributed
218 worldwide (Figure S1, STAR Methods) where multiple water depths were sampled (surface
219 [SRF]: 5 m average depth; deep chlorophyll maximum [DCM]: 17-188 m; and mesopelagic
220 [MES]: 200-1000 m). This extensive and standardized sampling of plankton diversity
221 encompasses large gradients in temperature, resource/primary production, and environmental
222 stability (Figure 1A). Using the taxonomic information retrieved from genomics and imaging
223 data (Table S1), we distinguished 12 Marine Plankton Groups (MPGs, Figure 1B, S1A, S2,
224 Table S2, STAR Methods) with different trophic modes (e.g., photosynthetic/mixotrophs vs.
225 non-photosynthetic/heterotrophs), different life history strategies (e.g., parasitic protists,
226 endophytosymbionts), or corresponding to highly dominant taxa having a significant
227 contribution to the marine food web (e.g., copepods).

228 The LDG of each MPG was studied using the Shannon index, a diversity index that relates
229 monotonically to species richness but differs in that it downweights rare species, whose
230 numbers are highly sensitive to undersampling and molecular artefacts (Figure S3; see STAR
231 methods). Focusing on surface waters first (SRF samples), we found that phyto-, bacterio- and
232 zooplankton MPGs all exhibited maximal MOTU diversity in tropical to subtropical regions
233 that then decreased poleward (Figure 2A, see also Figure S4 for individualized curves for
234 each MPG as well as for specific taxonomic groups). Similar trends were found for parasites
235 of eukaryotes (giruses and parasitic protists mainly composed of marine alveolates (MALV))
236 and for eukaryotic photosynthetic intracellular symbionts (endophytosymbionts) as well as
237 their eukaryotic hosts (photohosts). Different patterns emerged for two abundant families of
238 prokaryotic viruses (Myoviridae and Podoviridae) which, unlike their hosts, did not exhibit a
239 clear poleward decline in diversity. Because the diversity of hosts and their symbionts or
240 parasites is often assumed to be linked through eco-evolutionary interactions (Morand, 2015)
241 an explanation for this could be that these virus families have a broader spectrum of host
242 species, which could potentially decouple certain eco-evolutionary constraints (de Jonge et
243 al., 2019). However, other factors may be responsible for this trend as well, such as nutrient

244 availability or bacterial cell density (Gregory et al., 2019). Further data and analyses will be
245 necessary to elucidate the underpinnings of this result.

246 Differences in the form of LDGs have previously been proposed to result from contrasting
247 strategies in energy acquisition and processing (Hillebrand, 2004). To test this hypothesis, we
248 compared LDG forms across MPGs (except for prokaryotic viruses) by conducting a
249 segmented linear regression analysis and using the inferred parameters in a clustering analysis
250 (absolute latitudinal breakpoints and slopes of the segment regressions, STAR Methods,
251 Figure S5). Confirming our above assumption, parasites and endophotosymbionts did not
252 cluster directly with their hosts. Endophotosymbionts have extensive free-living populations
253 (Decelle et al., 2012) and parasitic protists might experience relatively long lasting free-living
254 stages under the form of resistant cysts waiting for host availability (Siano et al., 2010), which
255 could explain this result. Rather, we found that MPGs with similar broad trophic modes
256 (phototrophic vs. heterotrophic/chemotrophic) tended to exhibit similar LDG forms. However,
257 we noticed two particular exceptions: photosynthetic protists clustered with heterotrophs
258 (both prokaryotes and eukaryotes) while heterotrophic protists clustered with phototrophs.
259 Whether these features result from the presence of yet unknown mixotrophs in heterotrophic
260 protists (i.e., photosymbioses), or a preferential heterotrophy of mixotrophic photosynthetic
261 protists remains to be determined. Top-down or bottom-up controls by other trophic levels, as
262 well as interspecific competition could also contribute to these patterns. For example, most
263 copepods feed preferentially on phototrophic protists (e.g. diatoms or dinoflagellates; Saiz and
264 Calbet, 2011), which could explain why both groups exhibited similar LDGs (Figure S5).

265 We then examined the symmetry of the LDGs by performing separate linear regressions for
266 each hemisphere. LDGs are commonly observed to be steeper in the northern hemisphere,
267 supposedly due to stronger climate instability in this area of the globe (Chown et al., 2004).
268 Our results contradict this expectation, as we found that LDGs only tended to be asymmetric
269 and steeper in the southern hemisphere for archaea and photosynthetic protists (Figure 2A,
270 Table S3). While in agreement with another report on marine bacterioplankton (Sul et al.,
271 2013), we suspect the absence or opposite trend observed here to arise from a significant
272 undersampling at mid- to high latitudes in the southern hemisphere in our dataset (Figure S1).
273 Another explanation could lie in differences in the timing of sampling between the two polar
274 regions, i.e., from the end of spring to the beginning of autumn in the Arctic Ocean, but only
275 in a summer month in the Southern Ocean, when diversity is expected to be lowest due to
276 intense blooms (Arrigo et al., 2008). In spite of some variations in the form of LDGs across
277 MPGs or between hemispheres, our results nonetheless show that the poleward decline of
278 diversity is a pervasive feature among marine plankton.

279 To ensure that the MOTU diversity trends observed with our molecular data (Figure 2A) were
280 not biased by the DNA region studied or molecular approach used (i.e., DNA metabarcoding
281 vs. metagenomics for prokaryotes, (Salazar et al.; in press)), which may vary in taxonomic
282 resolution or overrepresent certain taxa, we compared them against those obtained with other
283 DNA markers (i.e. the V4 region of the 18S rRNA gene for eukaryotes, and the V4-V5

284 regions of the 16S rRNA gene for prokaryotes), or with finer clustering thresholds (see STAR
285 methods). All these comparisons exhibited high correlation coefficients values, regardless of
286 the clustering similarity thresholds used (Figure S6A-D). DNA-based measures of diversity
287 can also be affected by organism size (multicellular organisms) or gene copy number
288 (unicellular organisms), with organisms of smaller size or lower gene copy numbers being
289 likely more difficult to detect. To examine this potential issue, we compared the diversity
290 trends of different planktonic groups observed with molecular vs. optical data (Figure 2B-C,
291 see STAR methods). Both zooplankton imaging data, which consists in morphological
292 features (see Figure 2B for examples), as well as photosynthetic protist data obtained through
293 confocal (Colin et al., 2017) or light microscopy were all highly congruent with their
294 corresponding molecular-based diversity trends (Figure 2C, S6E-H). Although of much lower
295 taxonomic resolution, flow cytometry-based diversity values, comprising mainly prokaryotes,
296 also correlated well with molecular-based prokaryotic diversity (Figure 2C). These results,
297 together with the high correlation of diversity trends between our data and those based on
298 single copy genes (Milanese et al., 2019), and the fact that relative abundances in DNA-based
299 data correlate well with organism size/biovolume and even abundance at lower taxonomic
300 resolution (de Vargas et al., 2015), suggest that the global diversity trends observed here are
301 unlikely to be biased by differences in body size/gene copy number across taxa.

302 By contrast, we did not observe any LDG, neither in terms of MOTUs nor morphological
303 diversity, below the photic zone (>200 m depth, corresponding here to both mesopelagic
304 (*Tara* Oceans) and bathypelagic waters (Salazar et al., 2016); Figure 2D, S7). These
305 environments are isolated from sunlight and climatic gradients. Accordingly, while we did
306 observe a weak latitudinal trend in temperature in our deep sea samples (linear regression on
307 absolute latitudes: slope = -0.11, $R^2 = 0.273$, $p < 0.001$), the range of this parameter
308 represented roughly half of the temperature range present in surface waters (0 to 18°C vs. -2
309 to 31°C, respectively). Reduced temperature variations could hence be one of the reasons for
310 an absence of LDG in the deep sea. In addition, there is overall more carbon export at high
311 latitudes (Henson et al., 2012). This could compensate the reduction of diversity potentially
312 induced by low temperatures by increasing resource availability in polar deep waters
313 (Pomeroy and Wiebe, 2001). Finally, migration of surface species to deep waters through
314 passive or active vertical flux may also contribute to cancel out temperature effects, and
315 perhaps underpin the overall higher diversity values we observe in deep sea waters compared
316 to the surface (Figure 2C-D; Mestre et al., 2018). While the current sampling effort in these
317 aphotic environments is insufficient to firmly support these hypotheses, our results are
318 consistent with previous observations for brittle stars (Woolley et al., 2016) and bacteria
319 (Ghiglione et al., 2012) in the deep sea, whose diversity did not follow LDG trends. Both
320 sediments and water layers below the photic zone are populated by heterotrophic and
321 chemolithoautotrophic organisms, whose diversity and abundance are strongly influenced by
322 organic matter availability (Bergauer et al., 2018; Danovaro et al., 2016; Woolley et al., 2016).
323 This supports the idea that life is sustained by different types of energy supply across water
324 layers, from systems driven by solar energy or kinetic effects of temperature in epipelagic
325 waters, to chemically driven environments (i.e., carbon or mineral-based) in the deep sea.

327 *Global drivers of MPG diversity in the surface ocean*

328 To further understand the mechanisms underlying the observed LDGs in the surface ocean,
329 we considered contextual variables related to the most common LDG hypotheses. First, we
330 used sea surface temperature (SST, *in situ* measurements) to assess the “physiological
331 tolerance” and “kinetic energy” hypotheses. Second, we used chlorophyll *a* concentrations
332 (chl *a*, *in situ* measurements) and annual maximum of nitrate concentration (AM NO₃) to test
333 the “productivity/resources hypothesis”. Chl *a* was considered as a proxy for phytoplankton
334 biomass. We acknowledge the latter may be affected by the poleward increase of intracellular
335 pigmentation in phytoplankton to compensate limitations in light (Behrenfeld et al., 2015).
336 Phytoplankton carbon estimated via particulate backscattering has been proposed as a better
337 proxy (Graff et al., 2015), but we lacked this parameter for many stations. Nevertheless, the
338 available backscattering data exhibited a high correlation with chl *a* (Spearman’s $\rho = 0.6$, $p <$
339 0.001 , Figure S8). Regarding AM NO₃, the annual availability of this macronutrient is
340 fundamental for primary production (Moore et al., 2013). We therefore considered this
341 parameter to capture longer term effects of primary production on the observed plankton
342 diversity. Third, we considered intra-annual variation (IAV) of SST to test the “environmental
343 stability hypothesis”. In addition, we also included a set of other contextual parameters in our
344 analysis, in order to identify potential drivers of diversity patterns for MPGs that had not
345 previously been resolved (i.e., for viruses and protists; see STAR Methods for more details,
346 Figure S8). Among them, sunlight, which is the fundamental source of energy for
347 photosynthetic groups, was accounted as satellite-derived estimates of photosynthetically
348 active radiation (PAR) and the median light in the mixed layer (see STAR Methods). Their
349 more scattered availability in our dataset indicated high correlations with SST and mixed
350 layer depth, respectively (Figure S8), which together with chlorophyll *a* concentration reflect
351 well the light conditions at the different sampling stations.

352 We conducted a combination of correlation analyses and generalized additive models (GAMs,
353 Hastie, 2017), which allows to deal with non-linear and/or non-monotonic relationships that
354 could be found between diversity and environmental gradients (see below; see STAR
355 Methods). We restricted our analysis to surface planktonic communities due to their major
356 contribution to oceanic biogeochemical cycles (Falkowski et al., 2008; Field et al., 1998),
357 their greater sensitivity to climate change (Bopp et al., 2013), and because of greater *Tara*
358 Oceans data availability compared to the deep waters, hence allowing us to make more robust
359 inferences and projections.

360 We found that SST was strongly and positively associated with the MOTU diversity patterns
361 of most MPGs (Figure 3A-B, S9A) and, as such, was the best predictor of MPG diversity
362 amongst the parameters tested (Figure 3C). While new for most protist MPGs, these findings
363 are consistent with previous observations for bacterioplankton (Fuhrman et al., 2008),
364 copepods (Rombouts et al., 2009), and larger marine organisms (Tittensor et al., 2010;
365 Woolley et al., 2016). SST and species thermal tolerance limits have been suggested to

366 impose strong constraints on the distribution/abundance of marine ectotherms, including
367 copepods (Beaugrand et al., 2009; Sunday et al., 2012). Our results extend this explanation to
368 unicellular organisms as well, as we observed a decline of phototrophic bacteria (mainly
369 cyanobacteria) relative abundance at cooler higher latitudes (Figure 1B), while the relative
370 abundance of phototrophic eukaryotes (mainly diatoms) increased. Such differences may
371 result from contrasting thermal niches, as diatoms generally have larger thermal breadths and
372 lower minimal thermal growth than cyanobacteria (Chen, 2015). In the same line, the
373 temperature-diversity relationship of several MPGs increased until reaching a plateau, in
374 particular for heterotrophic bacteria and archaea (Figure S9A). This may suggest that these
375 groups have larger ranges of temperature optima, corresponding roughly to those encountered
376 in tropical/subtropical waters, and should be less affected by climate change (Hutchins and
377 Fu, 2017). Greater SST should also increase both speciation and extinction rates according to
378 the metabolic theory (reviewed in Brown, 2014). This assumption has been proposed for
379 marine foraminifera (Allen et al., 2006) and diatoms (Lewitus et al., 2018), suggesting that
380 temperature-dependent evolutionary processes are likely important in generating patterns of
381 diversity across MPGs. However, our current approach remains correlative, and future
382 phylogenetic studies will be critical to estimate speciation and diversification rates in relation
383 to temperature.

384 MPG diversity also decreased noticeably and monotonically with increasing standing stocks
385 of chl *a*, and to a lesser of AM NO₃ (Figure 3A-B, S9B-C). These negative relationships are
386 counterintuitive with the “productivity/resources hypothesis”, which asserts that greater
387 resource availability should promote species coexistence through niche partitioning. They also
388 contrast with the unimodal biomass-diversity relationship often reported for phytoplankton
389 (Irigoien et al., 2004; Li, 2002; Vallina et al., 2014). As explained above, it is very unlikely
390 that this difference arises from the diversity indices used (i.e., richness vs. Shannon index).
391 Rather, we explain this difference by our broader sampling of plankton size classes and the
392 increased detection and taxonomic resolution of our DNA-based identification methods.
393 Accordingly, our results are in agreement with taxon-focused or DNA-based surveys, which
394 have reported higher diversity of copepods (Rombouts et al., 2009), bacteria (Smith, 2007)
395 and microplankton (Raes et al., 2018) at sites of low primary production. While our data
396 preclude us to infer the exact mechanisms behind this negative relationship, we propose
397 several potential explanations. First, this observation may be related to the “paradox of the
398 plankton” (Hutchinson, 1961), i.e., the observation that a limited number of resources support
399 unexpectedly highly diverse communities. Non-equilibrium and chaotic environmental and/or
400 population dynamics in aquatic systems can occur at very small temporal and spatial scales,
401 and this, together with the existence of dormant stages in plankton organisms, are usually
402 thought to underlie this feature by preventing local extinction (Roy and Chattopadhyay, 2007;
403 Scheffer et al., 2003; Ser-Giacomi et al., 2018). Also, recent genomic studies in prokaryotes
404 suggest that adaptive gene loss and subsequent microbial feeding interdependencies are
405 selectively favored in aquatic, nutrient-poor environments. These dependencies would
406 constitute additional, yet currently unmeasurable niche axes, thereby supporting more species
407 (Giovannoni et al., 2014; the “black queen hypothesis”; Morris et al., 2012). More generally,

408 such trophic interdependencies probably do exist in the plankton trophic network without
409 necessarily involving genome streamlining. On the other hand, high nutrient or chl *a*
410 environments can correspond to areas with punctual/mid-term strong physical forcing, such as
411 winds (Demarcq, 2009) or changes in light availability, which we did not measure on site.
412 These environments are usually found to promote the growth of a few species at the expense
413 of others through competitive or trophic interactions (Behrenfeld and Boss, 2014; Huisman et
414 al., 1999; Irigoien et al., 2004; Li, 2002).

415 Intra-annual variation of SST (Figure S9D), as well as other abiotic parameters such as mixed
416 layer depth together with its intra-annual variation, silicate or phosphate concentrations
417 exhibited comparatively weak or no correlation with MPG diversity (Figure 3A-C, Table S4).
418 Finally, the GAMs including the four focus parameters (i.e., SST, chl *a*, IAV SST and AM
419 NO₃) did not exhibit latitudinal trends in their residuals (Table S5), hence suggesting that the
420 LDG was fully explained by these models. SST, followed by chl *a* concentration, thus appear
421 as prominent drivers of plankton diversity. This conclusion is further supported by additional
422 GAMs where only SSTs, chl *a* concentrations, and their interaction were used as explanatory
423 variables (see STAR methods and their further use below). These latter models had
424 exceptionally high explanatory power for most MPGs (42 to 81% of deviance explained), and
425 also successfully explained the LDGs (Table S6-7). In addition, SSTs strongly correlated with
426 microbial and photosynthetic abundances, and chl *a* strongly correlated with abundances of
427 larger metazoans (Figure 3A, Figure S10A-B). This supports the idea that these two
428 parameters regulate MPG diversity by controlling their population size and, therefore, also
429 their extinction rates (Clarke and Gaston, 2006). Thus, our results lend support to the interplay
430 of “physiological tolerance”, “kinetic energy” and to a lesser extent of
431 “productivity/resources” effects in regulating MPG diversity in planktonic communities and
432 causing latitudinal gradients of diversity in epipelagic waters.

433 While our overall conclusions concur with those reported for marine macroorganisms
434 (Hillebrand, 2004; Tittensor et al., 2010; Woolley et al., 2016), they partially contrast with
435 recent findings for planktonic communities in the South Pacific Ocean (Raes et al., 2018),
436 where primary productivity has been found to override temperature effects. This difference
437 could be a consequence of the sampling extent of our study, which covers both northern and
438 southern hemispheres as well as multiple oceanic provinces that may differ in their diversity
439 gradient (Chown et al., 2004; Sul et al., 2013). By contrast, Raes et al. (2018) characterized
440 the latitudinal trends along a transect exhibiting marked environmental transitions caused by
441 subtropical and subpolar waterfronts. This should be confirmed by analysing a larger number
442 of sampling points in each basin than those available here. Another possible explanation lies
443 in the different diversity measures used in the two studies. The Shannon index used here,
444 albeit co-varying with species richness, downweights the influence of rarest species. The
445 carrying capacity of a given environment strongly relies on resource availability and primary
446 productivity, which therefore control local extinction, in particular of rare species (Vallina et
447 al., 2014). Such processes can solely be detected with species richness, which we did not
448 assess here due to its strong sensitivity to sampling and technical biases (STAR methods).

449 More generally, several factors are also more confounding at the global scale, and their effects
450 more difficult to tease apart. For example, SST partially correlates with chl *a* concentration,
451 PAR, annual averages and intra-annual variations in solar radiation, as well as with the length
452 of the productive season at the global scale (Figure S8; Clarke and Gaston, 2006). It is hence
453 possible that both resource/sunlight-energy availability and stability effects contribute
454 partially to the observed temperature effects. This feature may also explain why we could not
455 find clear clustering of MPGs based on the drivers of their diversity according to their broad
456 trophic modes, as found for their LDG patterns (Figure S5). Finally, we acknowledge that we
457 considered environmental stability over short time scales. Past glaciation cycles and
458 associated sea level changes do most likely contribute to current MPG diversity, as suggested
459 for marine diatoms (Lewitus et al., 2018) and foraminifera (Yasuhara et al., 2012).
460 Notwithstanding, fossil records do suggest that the poleward decline of zooplankton diversity
461 and its temperature dependence is a remarkably stable feature through geological times
462 (Yasuhara et al., 2012), albeit with variations in the overall levels of diversity. We hence
463 believe that paleoclimate effects are unlikely to alter our conclusions.

464

465 *Future global trends of MPG diversity*

466 Climate change scenarios predict a general increase of SST, with major changes in the Arctic
467 Ocean (Figure S11; Pachauri et al., 2014). Future ocean primary production is expected to
468 decrease in the northern hemisphere and to increase in the Southern Ocean, although these
469 projections are more uncertain (Figure S11; Bopp et al., 2013). To search for trends in
470 diversity variation in response to these changes, we mapped the MOTU diversity of several
471 MPGs at the beginning (years 1996-2005; Figure S12) and end of the 21st century (2090-
472 2099) under a scenario of severe climate warming (RCP 8.5; see STAR Methods). We used
473 SST and chl *a* concentration values simulated by Earth System Models of the Coupled Model
474 Intercomparison Project Phase 5 (CMIP5; Bopp et al., 2013; see Table S8) and GAM models
475 from epipelagic plankton that explained $\geq 60\%$ of deviance (6 MPGs out of 12, Table S6).
476 After ensuring that SST and chl *a* simulated values were within the range of values used to
477 train our models, we projected current and future MPG diversity at the global scale and
478 calculated diversity anomalies (i.e., percentage of diversity change) between contemporary
479 and future climates to identify areas where plankton diversity is most likely to be affected by
480 the environmental changes in the ocean (Figure 4, S12). To ensure reliability of our
481 predictions, we generated 13,000 models for each MPG and each projection time so as to
482 account for the uncertainties in the parameters of the GAMs and the output from different
483 CMIP5 models used in this study (see STAR methods). We here report averaged predictions
484 from these models (see Figure S12 for prediction uncertainties). We also cross validated our
485 GAM models with independent data sets from other studies (STAR methods; Figure S13), and
486 obtained predictions congruent with the observed diversity.

487 Our projections suggest a general increase of MPG diversity, in particular in the northern
488 hemisphere and at latitudes that encompass the limits of the subtropical gyres (25° - 50°)

489 (Figure 4A, S12). These results support a tropicalization of temperate planktonic diversity or
490 biomass, as suggested previously for bacterioplankton (Morán et al., 2010, 2017),
491 zooplankton (Beaugrand et al., 2015), and also fish (Cheung et al., 2013; Vergés et al., 2016).
492 Following SST trends, the most dramatic changes in diversity across most MPGs are expected
493 to occur in the Arctic Ocean (more than 100% average increase over latitude, Figure 4B). In
494 this biome, copepods and photosynthetic bacteria should experience the most dramatic
495 increases in diversity, mostly because these communities are currently poorly diverse. The
496 low abundances of endophotosymbionts resulted in them exhibiting a large relative increase
497 in diversity as well, especially at high latitudes (for absolute anomalies values see Figure
498 S12). All these observations are in line with the poleward range expansion predicted for
499 phytoplankton (Barton et al., 2016), in particular the cyanobacterial group *Synechococcus*
500 (Flombaum et al., 2013), as well as for boreal fish species (Frainer et al., 2017), as a short-
501 term response to poleward shifts in thermal niches (Thomas et al., 2012).

502 Hence, epipelagic planktonic communities are predicted to be strongly affected in the future,
503 primarily by rising temperatures. Changes in chl *a* (higher uncertainty), either bound to
504 primary production or photo-acclimation (Behrenfeld et al., 2015), should have more
505 secondary effects except in restricted areas for heterotrophic bacteria and marine copepods,
506 where their effects seem to override those of SST (Figure S12D). In any case, the changes in
507 MPG diversity predicted to occur by the end of the century will most probably induce
508 cascading changes over the entire marine food web, e.g., by causing trophic mismatches or
509 altering host-parasite/symbiont interactions (Doney et al., 2012; Edwards and Richardson,
510 2004; Gilg et al., 2012). For example, the increase in diversity and abundance of phototrophic
511 bacteria suggested by our results and others (Hutchins and Fu, 2017) would reduce upward
512 energy flow in marine food webs, as these taxa are usually less palatable for higher trophic
513 levels (Ullah et al., 2018). Likewise, increased temperature and diversity may also lead to
514 reduced organism body size (Sommer et al., 2017). If the diversity and abundance of small-
515 bodied organisms are to increase, this may again reduce the energy transfer to higher trophic
516 levels (Beaugrand et al., 2008).

517 Finally, we assessed the current ocean socio-economic and conservation status of most-
518 impacted latitudes in terms of MPG diversity (i.e., the 25% of latitudes with highest mean
519 absolute diversity anomalies). We did so by quantifying the current particulate carbon export,
520 the maximum marine fisheries catch, and the number of marine protected areas at each
521 latitude relative to global average expectations. We found that most-impacted latitudes in the
522 future exhibit currently higher fisheries catch (32-70% above the average), carbon export (23-
523 70% above the average), and fraction of marine protected areas (up to 100% above the
524 average; Figure 4B, Table S9). This raises the question of how changes in diversity under the
525 most severe climate warming scenario will impact global biogeochemical processes such as
526 carbon export and sequestration, which are believed to have already been affected by climate
527 change (Brun et al., 2019) and what would be the consequences for marine life in general,
528 from already vulnerable marine animals and fish landings to life in the deep sea.

530 Concluding remarks

531 The present findings and projections need however to be interpreted carefully. Although being
532 the largest systematic sampling effort of the oceanic plankton to date, our sampling is limited
533 by its punctual nature both in space and time. Our models are also correlative and do not
534 directly account for the effects of other abiotic parameters, such as *in situ* solar irradiance and
535 their seasonal variations, as well as of biotic interactions and their dynamics, which should all
536 influence plankton diversity. Regarding our projections, there are strong uncertainties about
537 the potential lag between environmental changes and the response of plankton diversity, as
538 well as on the adaptation potential of planktonic species to climate change, which can be
539 relatively rapid as recently proposed for zooplankton (Peijnenburg and Goetze, 2013) and
540 diatoms (Schaum et al., 2018). Further studies accounting better for these different and
541 intertwined mechanisms that operate at multiple spatial and temporal scales will be
542 instrumental to improve our understanding of the drivers underlying ocean plankton
543 ecosystems and their feedbacks with global change. Nevertheless, our approach is a first
544 attempt to embrace this biological complexity at the global scale and our results broadly agree
545 with other statistical or theoretical projections (Barton et al., 2010, 2016; Righetti et al., 2019;
546 Rombouts et al., 2009; Thomas et al., 2012; Tittensor et al., 2010). Our results should hence
547 be seen as a baseline and a framework for testing new hypotheses about changes in diversity
548 within the whole plankton community across the global ocean, identifying the most
549 vulnerable areas, and to better appreciate and anticipate functional and socio-economic
550 consequences (Cavicchioli et al., 2019). These results will hence be of help in guiding future
551 broad and macroscale strategies to mitigate the effects of climate change on marine diversity
552 and ecosystem services.

553

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592

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608

609 **Declaration of Interests**

610 The authors declare no competing interests.

611

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666 **Main figure titles and legends**

667 **Figure 1: Latitudinal trends of oceanic conditions and marine plankton composition in**
668 **surface waters.** (A) *in situ* chlorophyll *a* concentrations and sea surface temperatures (SST)
669 across latitude (*Tara* Oceans expedition), plus intra-annual variation (IAV) of SST (NOAA,
670 ERSST v5). Solid lines represent the GAM smooth trends and grey ribbons the corresponding
671 95% confidence intervals of parameters latitudinal trend predicted by the GAMs. (B) Average
672 relative abundances of MPGs as inferred from molecular datasets across latitude. Prokaryotes:
673 16S rRNA gene, 0.22-3 μm . Eukaryotes: 18S rRNA gene, 0.8-2000 μm (STAR Methods).
674 Dark grey represents other eukaryotic groups. P: photosynthetic/mixotrophic. H: non-
675 photosynthetic/heterotrophic. The three viral groups are not represented here due to absence
676 of comparable abundance data. See also Figures S1-S2 and Tables S1-S2.

677 **Figure 2: Latitudinal patterns of marine plankton diversity.** (A) LDGs at the sea surface
678 for all MPGs. P: photosynthetic/mixotrophic; H: non-photosynthetic/heterotrophic (see STAR
679 Methods). (B) Morphological diversity as analysed from >77,000 organisms collected with
680 the bongo net (Imaging | 300 μm). Morphological measurements were normalized and
681 subjected to a t-SNE ordination analysis using all samples (see STAR Methods). In the central
682 2D t-SNE ordination, each dot corresponds to an organism, and its color to its taxonomic
683 assignation (>100 taxa). For ease of figure interpretation, the points corresponding to a subset
684 of abundant groups are displayed separately. The three t-SNE ordinations displayed on the
685 right show dots from three stations distantly located and from different latitudes, as shown in
686 the map. Six images are also presented as examples of the underlying data (see STAR
687 Methods); 1 mm scale bars are shown below each picture. (C/D) Patterns of the whole
688 plankton community using different sampling protocols, at (C) the sea surface
689 (16S/18S/FC/LM) or a larger integrative depth of 500 m (Imaging), and (D) in mesopelagic
690 (average depth 540 m) or bathypelagic layers (BAT, average depth 4000 m, Malaspina
691 expedition). In all cases, solid lines correspond to GAM smooth trends and grey ribbons to the
692 95% confidence intervals of the Shannon latitudinal trend predicted by the GAMs (see also
693 Figures S4 and S7 for individual curves and explained deviance). Note that these trends are
694 drawn for illustrative purposes and were not used in downstream analyses. '16S' and '18S'
695 refer to the different rRNA subunit genes used as marker genes for metagenomics and
696 metabarcoding, respectively. 'Imaging' refers to the identification method for large eukaryotes
697 captured with nets. 'FC' refers to flow cytometry for the picoplankton, and 'LM' to light
698 microscopy-based survey of microphytoplankton (see STAR Methods). Numbers refer to the
699 filter mesh size.

700 **Figure 3: Drivers of plankton diversity in the surface ocean.** (A) Correlation of contextual
701 variables (abiotic and population densities; x-axis) with the Shannon index of each MPG (y-
702 axis). The color gradient corresponds to the values of the Spearman ρ correlation coefficient,
703 while the dot size to their absolute value. Labels of the x-axis are ordered according to a
704 hierarchical clustering analysis of absolute Spearman ρ correlation coefficient values between
705 each pair of contextual variables, whose corresponding dendrogram is shown in the upper part

706 of the plot. Yellow leaves correspond to the four variables analysed in (B-C), also underlined
707 below. Variables that do not cluster above the dotted line ($|\text{Spearman's } \rho| < 0.6$) are considered
708 as non-collinear. Percentages of 'Pico', 'Nano' and 'Micro' refer to the relative abundances of
709 fractions of phytoplankton based on pigment analysis. Bacteria and picoeukaryote abundances
710 were determined by flow cytometry, while 'Imaging' abundances refer to counts of
711 individuals caught by nets (STAR Methods). IAV: intra-annual variation; MLD: mixed layer
712 depth; SST: sea surface temperature. See also Figure S8. (B) Individual explained deviance
713 (color gradient and dot size) of four variables (see also Figure S9), and (C) additive
714 contribution of the same four variables to the total explained deviance in GAMs with the
715 Shannon index as response variable (see STAR Methods and Tables S4-S5). In A and B, non-
716 significant coefficients or effects are not shown. In C, significant effects are indicated with
717 asterisks. MPG labels are always ordered according to a hierarchical clustering analysis after
718 a Spearman correlation analysis based on the displayed values in each case, A-C.

719 **Figure 4: Projected changes in Shannon diversities by the end of the 21st century.** (A)
720 Projected changes by the end of the 21st century relative to the beginning of the century (%)
721 for MPGs accounting for GAM models with high explained deviance (>60%). Projections
722 were based on SST and chl *a* data simulated by the CMIP5 models and the GAMs ($n = 13,000$)
723 for each combination of MPG and time frame; see STAR Methods and Tables S6-8; see
724 Figures S12 for standard deviation by grid-cell). Copepods, photosynthetic protists, parasitic
725 protists and endophotosymbiont diversity (Shannon index) was modeled based on 18S rRNA
726 gene metabarcoding data, size fraction 0.8-2000 μm , and diversity of heterotrophic and
727 photosynthetic bacteria on 16S rRNA gene metagenomics data, size fraction 0.22-3 μm , all
728 from the surface layer. Predicted Shannon values ≤ 0 obtained at high latitudes, particularly
729 for copepods and endophotosymbionts, were excluded. (B) Latitudinal averages of values in
730 (A) and their uncertainties. For visualization purposes in (B), average anomalies for
731 endophotosymbionts and copepods were drawn up to latitudes where values remain below
732 100%, and all plots show the averaged standard deviation reduced by half. Note also that the
733 x-axis is not fixed. The last three panels refer to latitudinal averages of particulate organic
734 carbon (POC) export at 100 m (Henson et al., 2012); number of grid-cells with high marine
735 fisheries catch (>200 kg km⁻² yr⁻¹) (Watson, 2017); and marine protected areas (MPAs)
736 latitude kernel density plot (Bruno et al., 2018; see STAR Methods and Table S9).

737

738

739 **Supplemental figure title and legends**

740 **Figure S1. Tara Oceans stations and Shannon diversity patterns. Related to Figures 1**
741 **and 2.** (A) MPGs at the sea surface (< 5 m depth), (B) whole planktonic community using
742 different sampling protocols at the sea surface (except for “Imaging”, integrative depth from
743 500 m depth to the surface) and (C) whole planktonic community of the mesopelagic realm
744 (200-1000 m depth). Number of stations are specified in the inset titles. Color represents the
745 Shannon index. For more details on the different size fractions and sampling protocols, please
746 refer to the caption in Figure 1 and STAR Methods.

747 **Figure S2. Average abundances of a broader list of plankton groups across latitude.**
748 **Related to Figure 1 and 2.** For 18S rDNA metabarcodes (relative abundances), imaging from
749 net catches and flow cytometry (absolute abundances). Numbers refer to the filter mesh size
750 (μm). H: non-photosynthetic/heterotrophic, P: photosynthetic/mixotrophic. See Figures 1 and
751 S1 for further sampling details. The three viral groups are not represented here due to absence
752 of comparable abundance data. Note that the differences between protocols relate, amongst
753 other things, to resolution (e.g., potential photohosts from the nets are classified as Protists
754 (H)), marker gene copy number (e.g., high in photohosts), lack of detection (many small
755 copepods are lost when sampling with nets), or water column sampling differences
756 (SRF/DCM vs. INT for molecular/cytometry vs. net catches, respectively).

757 **Figure S3. Rarefaction curves for the plankton community. Related to Figure 2 and**
758 **STAR Methods.** Based on richness (A, C) and Shannon (B, D), for prokaryotes (16S rRNA
759 gene miTags, A, B), and eukaryotes (18S rRNA gene V9 metabarcoding, C, D). Each line
760 corresponds to a surface water sample. Colors correspond to different latitudinal bands
761 (absolute values).

762 **Figure S4. Sea surface latitudinal gradient of diversity. Related to Figure 2A.** (A) For
763 viral, prokaryotic and eukaryotic MPGs, and (B) for well-known protist phyla and the
764 dominant class of bacteria, Alphaproteobacteria, for which ~50% corresponds to the SAR11
765 clade. Solid lines represent the GAM smooth trends and grey ribbons the corresponding 95%
766 confidence intervals of the Shannon latitudinal trend predicted by the GAMs. The percentages
767 provided below inset titles correspond to the deviance explained by GAMs when significant.
768 Viruses and bacterial diversities are inferred from samples filtered at 0.22-3 μm and analysed
769 through marker genes derived from metagenomics. Eukaryote diversity shown here is inferred
770 from 18S rDNA metabarcoding of samples filtered at 0.8-2000 μm . H: non-
771 photosynthetic/heterotrophic, P: photosynthetic/mixotrophic.

772 **Figure S5. Classification of MPG sea surface LGD analysed by segmented regression.**
773 **Related to Figure 2A.** The estimated break is the absolute latitude between the two segments
774 of slope s_1 and s_2 , respectively. We used pink lines for $s_1 \leq 0$ (plateau or peak around the
775 equator) and blue lines for $s_1 > 0$ (extra-equatorial peak). The dendrogram is the result of a
776 hierarchical clustering based on the differences in break and slope values across MPGs
777 (Euclidean distance on standardized values).

778 **Figure S6. Correlation between the Shannon values derived from multiple datasets of**
779 **Tara Oceans. Related to STAR Methods.** (A) OTUs (as defined with “swarm”, Mahé et al.
780 2014) obtained with the V9 (x-axis) and V4 (y-axis) regions of the 18S rRNA gene using
781 surface water samples (SRF); size fraction 0.8-2000 µm; (B) OTUs either as defined with
782 swarm (x-axis) or defined at 100% sequence identity from the V9 region of the 18S rRNA
783 gene for SRF samples, size fraction 0.8-2000 µm; (C-D) 16S rRNA gene miTags (x-axis) vs.
784 OTUs defined at 97% [C] and 100% sequence similarity [D] (y-axis) obtained from the V4-
785 V5 regions of the 16S rRNA gene for SRF samples, size fraction 0.22-3 µm. (E) OTUs of
786 photosynthetic protists obtained with the V9 region of the 18S rRNA gene (x-axis) vs. protists
787 (mostly photosynthetic) as identified with environmental High Content Fluorescence
788 Microscopy (eHCFM, data from Colin et al., 2017) in SRF-DCM samples, size fraction 5-20
789 µm; (F) Diatom OTUs obtained with V9 region of the 18S rRNA gene (x-axis) vs. diatoms
790 species counted by light microscopy (y-axis) in SRF samples; size fraction 20-180 µm; (G/H)
791 Copepods OTUs obtained with the V9 region of the 18S rRNA gene, SRF samples, size
792 fraction 180-2000 µm (x-axis) vs. abundances [G] and biovolumes [H] of copepods collected
793 by the WP2 net, >200 µm. Inset titles show the Pearson’s correlation coefficient and its
794 associated p-value. Note the differences in axes scales. Dashed line represents 1:1 relation.
795 Refer to STAR Methods for details on each method.

796 **Figure S7. Latitudinal gradient of diversity across size and depth. Related to Figures 2B-**
797 **D.** For the whole prokaryotic (16S miTags, 0.22-3 µm, and 16S OTUs, 0.2 µm for
798 bathypelagic (BAT)) and eukaryotic communities (18S OTUs, 0.8-2000, 20-180 and 180-
799 2000 µm; imaging, >300 and >680 µm) at different depths (SRF: surface, < 5 m; DCM: deep
800 chlorophyll maximum, 17-188 m, and MES: mesopelagic, > 200 m, BAT: bathypelagic, >
801 4000 m, INT: integrative, depth from 500 m depth to the surface). Non-significant GAMs are
802 denoted with “NS”. See Figure S4 legend for more information on the plot. Note that the
803 particular trend for the regent net, i.e. Imaging | 680 µm might be due to undersampling of
804 small zooplankton.

805 **Figure S8. Multiple pairwise Spearman correlation analysis of the full matrix of**
806 **contextual parameters for the surface ocean. Related to Figure 3A.** Rows and columns
807 were clustered based on the absolute pairwise Spearman correlation turned into distance ($1 -$
808 $|\rho|$). MLD: mixed layer depth. E_median ML: median light in the mixed layer. IAV: intra-
809 annual variability. Part.backscat.coef: particle backscattering coefficient. For more
810 information on parameters, see Figure 3 and STAR Methods.

811 **Figure S9. Relationships between diversity and 4 contextual variables for viral,**
812 **prokaryotic and eukaryotic MPGs. Related to Figure 3B.** (A) SST, (B) chl *a*, (C) AM NO₃,
813 and (D) IAV SST. Solid lines represent the GAM smooth trends and grey ribbons the
814 corresponding 95% confidence intervals of the x-y relationship predicted by the GAMs. The
815 percentages provided below inset titles correspond to the deviance explained by GAMs when
816 significant (p-value corrected for multiple comparisons). Non-significant GAMs are denoted
817 with “NS”.

818 **Figure S10. Relationship between plankton abundance and two contextual variables.**
819 **Related to Figure 3A.** (A) SST, (B) chl *a*. Abundance values were obtained with flow
820 cytometry (reported in [cells/ml]) or from counts of individuals captured with nets of different
821 mesh size and identified by imaging (reported in [individuals/m³]), respectively. Solid lines
822 represent the GAM smooth trends and grey ribbons the corresponding 95% confidence
823 intervals of the X-Y relationship predicted by the GAMs. The percentages provided below
824 inset titles correspond to the deviance explained by GAMs when significant.

825 **Figure S11. Projected latitudinal changes in SST and chl *a*.** **Related to Figures 4 and S12.**
826 Anomalies (%) in (A) SST and (B) chl *a* at the end of the 21st century (2090-2099, RCP 8.5)
827 relative to the beginning of the century (1996-2006). Data was obtained from 13 CMIP5
828 models (Table S8). Grey ribbons represent the standard error.

829 **Figure S12. Modeled patterns of diversity of MPGs in the global ocean.** **Related to**
830 **Figure 4.** (A) Shannon index modelled at the global scale for oceanic conditions at the
831 beginning of the 21st century (1996-2006). Predicted Shannon values ≤ 0 obtained at high
832 latitudes, particularly for copepods and endophotosymbionts, were excluded. (B) Anomalies
833 were calculated as the difference of their Shannon index at the end (2090-2099, RCP 8.5) and
834 the beginning of the century (1996-2006). A positive value means that diversity will increase
835 by the end of the century. Note that the scale is not symmetric and that white means zero
836 change. (C) Uncertainty maps (standard deviation) for (B). (D) Areas where the effect of chl *a*
837 on plankton diversity is likely to be higher than the one of SST. To determine this, either chl *a*
838 or SST were held constant in the projections by the end of the century. Then, if the anomaly
839 caused only by the change of chl *a* was different than zero and higher (absolute terms) than
840 the one caused only by the change in SST, the pixel was colored. (E) Latitudinal diversity
841 gradient at the beginning (solid line) and the end (dashed line) of the 21st century. Values
842 represent averages over longitude for each latitudinal degree. Dots are observed values
843 (Figure 2). 13 Earth system models from CMIP5 were used (Table S8).

844 **Figure S13. Correlation between the Shannon values observed in independent datasets**
845 **and those for the same locations that are predicted by GAM models built in this work.**
846 **Related to STAR Methods.** (A) Heterotrophic bacteria from the surface, open ocean water
847 sites of the International Census of Marine Microbes (ICoMM; Zinger et al. 2011). (B)
848 Eukaryotic community retrieved from Raes et al. 2018. Note that for the latter the mesh size
849 of the filters used were not exactly the same (*Tara* Oceans > 0.8 μm ; Raes et al. > 0.22 μm).
850 Note also that both datasets have different sampling dates and locations in relation to *Tara*
851 Oceans. In both cases we used as predictors the temperature and chl *a* of each site predicted
852 by 13 CMIP5 models at the month of sampling averaged over 1996-2006. Inset titles show the
853 Pearson's correlation coefficient and its associated p-value.

854

855 **STAR Methods**

856

857 **Physical and environmental measurements**

858 Measurements of temperature, conductivity, salinity, depth, pressure and oxygen were carried
859 out at each station with a vertical profile sampling system (CTD-rosette) and Niskin bottles
860 following the sampling package described in Picheral et al. (2014). Chlorophyll *a* (chl *a*)
861 concentrations were measured using high-performance liquid chromatography (Ras et al.,
862 2008; Van Heukelem and Thomas, 2001). Phosphate and silicate concentrations were
863 determined using segmented flow analysis (Aminot et al., 2009). The contribution of three
864 pigment size classes (micro-, nano-, and picoplankton) to the total phytoplankton biomass was
865 estimated based on high pressure liquid chromatography (HPLC) analyses (Uitz et al., 2006).
866 A full description of the performed measurements is described in (Pesant et al., 2015).
867 Contextual data from the *Tara* Oceans expedition, including those that are newly released
868 from the Arctic Ocean, are available at <https://doi.org/10.1594/PANGAEA.875582>. Finally,
869 we complemented these *in situ* measurements with (i) the average intra-annual variation of
870 sea surface temperature (IAV SST) between years 1997-2017, which we obtained from the
871 Extended Reconstructed Sea Surface Temperature v5 (Huang et al., 2017), (ii) the annual
872 maximum of nitrate concentration (AM NO₃) retrieved from the World Ocean Atlas 2009
873 (Garcia et al., 2010), (iii) the intra-annual variation of the mixed layer depth (IAV MLD),
874 which was derived from a monthly climatology (Holte et al., 2017), (iv) iron levels, which
875 were derived from a global circulation model (Menemenlis et al., 2008), and (v) median
876 sunlight in the mixed layer, which was estimated as in Behrenfeld et al. (2015).

877

878 **Sample collection**

879 Samples were derived from 189 stations over the 210 surveyed during the *Tara* Oceans
880 expedition (2009-2013, Figure S1). They were collected across all major oceanic provinces
881 using the sampling strategy and methodology described in Pesant et al. (2015). Briefly, the
882 sampling was conducted at different water depths, i.e., at the sea surface (SRF, <5 m), the
883 deep chlorophyll maximum (DCM, 17-188 m) and the mesopelagic realm (MES, 200-1000
884 m). Sampling of the full, trans-kingdom planktonic diversity was performed with different
885 protocols depending on their post processing, i.e., either for DNA-based analyses or for
886 imaging analyses.

887 For samples dedicated to DNA analyses, we maximised the taxonomic breadth of our
888 diversity assessment by fractionating planktonic communities from pumped seawater with
889 filters of different mesh size. We considered samples collected with filters of 0.22-1.6/3 µm
890 (hereafter 0.22-3 µm) for viruses and bacteria (prokaryotic viruses from the filtrate, giruses
891 and bacteria from the 0.22 µm filter), and 0.8-2000 µm (0.8-3 µm for non-Arctic MES

892 samples), 5-20 μm , 20–180 μm and 180–2,000 μm for eukaryotes. Prokaryotic viruses were
893 flocculated using iron chloride (John et al., 2011). Preliminary analyses showed that the
894 samples obtained at 0.8-2000 μm mesh size were representative of the whole structure and
895 diversity of protists and even of copepods, whose high dominance allowed a straightforward
896 detection by this protocol too, probably due to the presence of small life-stages or individuals,
897 pieces of large ones, extracellular DNA from cell turnover, or fecal pellets. We hence
898 restricted our analysis of the main eukaryotic planktonic groups on this particular subset of
899 samples, but also provide diversity estimates at the scale of the whole eukaryotic planktonic
900 community for each filter size to support the robustness of the results.

901 Imaging data acquisition followed different protocols depending on the organisms targeted.
902 First, microphytoplankton were sampled at the sea surface with nets of 20-180 μm mesh size
903 for microscopy analyses (see below), as described in (Malviya et al., 2016). Large protists and
904 metazoans were collected with four different nets: WP2, bongo and Regent, with mesh sizes
905 of 200, 300 and 680 μm , respectively, which were towed vertically from 500 m to the surface.
906 We also used a multinet, with mesh size of 300 μm , from which only the deepest level
907 matching the mesopelagic realm was analysed (Pesant et al., 2015). Picoplankton samples
908 were prepared for flow cytometry from three aliquots of 1 ml of seawater (pre-filtered through
909 200- μm mesh), as described in Hingamp et al. (2013) and Sunagawa et al. (2015). Finally, we
910 made use of data derived from the Malaspina expedition (Salazar et al., 2016) to account for
911 diversity patterns of free-living prokaryotes in the bathypelagic realm (Figure 2D, S7). It
912 should be noted that the numbers of stations and samples examined varied according to the
913 combination of protocol and size fraction being analysed (Figure S1, Table S1).

914

915 **Plankton classification, diversity and abundance estimates**

916 A combination of molecular and optical methods were used to describe the planktonic
917 diversity of the ocean. A full description of the molecular data production is available in
918 Alberti et al. (2017). Viral and prokaryotic metagenomes were obtained by shotgun
919 metagenomics, for which sequencing, assembly and/or annotation are described in Gregory et
920 al. (2019) for bacterial and archaeal DNA viruses, Hingamp et al. (2013) for nucleo-
921 cytoplasmic large DNA viruses (i.e., giruses, also referred to as NCLDVs or giant viruses in
922 the literature), and Sunagawa et al. (2015) for bacteria and archaea.

923 Two families of prokaryotic viruses, Myo- and Podoviridae, were studied on the basis of a
924 capsid protein gene (*gp23*) and a DNA polymerase (*polA*), respectively (Adriaenssens and
925 Cowan, 2014). We kept populations with a *gp23/polA* match either via annotation (Pfam,
926 InterProScan and KEGG) or a set of *in silico* primers to increase the sensitivity (Adriaenssens
927 and Cowan, 2014), and their abundance corresponded to the normalized number of reads that
928 mapped against these genes. Analogously, the diversity of giruses was based on another DNA
929 polymerase gene, *polB*, specifically recruited with pplacer (Matsen et al., 2010) from a non-
930 redundant gene catalog (OM-RGCv2; Salazar et al. in press). The corresponding frequency

931 data was obtained by mapping the raw reads to the gene catalog. Note here that ssDNA and
932 RNA viruses were not analysed.

933 Prokaryotic taxa were defined on the basis of metagenomic reads that contained signatures of
934 the 16S rRNA genes (referred to as miTags; Logares et al., 2014; Salazar et al., in press; data
935 accessible at <http://www.ocean-microbiome.org>). Briefly, miTags were mapped to cluster
936 centroids of taxonomically annotated 16S/18S reference sequences from the SILVA database
937 (Pruesse et al., 2007) (release 128: SSU Ref NR 99) that had been clustered at 97% sequence
938 identity beforehand using USEARCH v9.2.64 (Edgar, 2010). Mapping of miTags to a unique
939 reference sequence were used to compute the abundances of MOTUs. A MOTU abundance
940 table was built by counting the number of miTags assigned to each reference sequence in each
941 sample. The abundance table was normalized by the total sum for each sample after excluding
942 MOTUs that corresponded to eukaryotes and chloroplasts.

943 Additionally, we analyzed data obtained by amplicon sequencing of the V4-V5 region of the
944 16S rRNA gene (primers 515F-Y and 926R; Parada et al., 2016), following the pipeline
945 described in https://github.com/SushiLab/Amplicon_Recipes. Briefly, paired-end reads were
946 merged at a minimum 90% of identity, and those with ≤ 1 mismatches were selected. Primer
947 matching was performed with CUTADAPT v.1.9.1. Dereplication, MOTU clustering at 97%
948 (UPARSE algorithm) and zOTUs denoting 100% similarity (UNOISE algorithm) were
949 performed with USEARCH v.10.0.240 (Edgar 2010). OTUs and zOTUs were taxonomically
950 annotated against the SILVA database v132 (Quast et al. 2013) with the Last Common
951 Ancestor approach. Non-prokaryotic MOTUs (eukaryotes, chloroplast and mitochondria)
952 were removed, whereas singletons were maintained. This dataset was used to ensure that the
953 diversity estimates obtained with metagenomics and amplicon sequencing approaches were
954 consistent (see below; see Figure S6). For flow cytometry data we defined six different
955 groups: low and high nucleic acid-content heterotrophic bacteria, *Prochlorococcus*,
956 *Synechococcus* and two groups of picoeukaryotes (see table of Data and Resources). This
957 latter set of samples was mainly used to determine the cell density of each
958 bacterial/picoeukaryote group, which we considered as contextual data in downstream
959 analyses. Nevertheless, we also retrieved diversity values from these data in order to assess
960 their congruence at broad scale with those obtained through molecular approaches. They were
961 not used to standardize DNA-based taxa abundances.

962 The taxonomic composition of protists and small metazoan communities was characterized
963 through DNA metabarcoding using mainly the V9 region of the 18S rRNA gene, and the V4
964 region was also used to assess the congruence of the MOTU diversity estimates between the
965 two DNA markers (Figure S6). For both sequencing reads datasets, we obtained a list of
966 MOTUs as defined by the “swarm” algorithm (Mahé et al., 2014). Each MOTU was
967 represented by a number of sequencing reads, which we used as a proxy for abundance. A full
968 description of the sequencing reads processing (i.e., data curation, clustering into MOTUs,
969 taxonomic classification, etc.) is available at <http://taraoceans.sb-roscoff.fr/EukDiv/>.
970 Microphytoplankton were also identified and quantified manually using an inverted light

971 microscope, as described in (Malviya et al., 2016). The identification was performed by
972 experts and reached the genus level for most of the 440 morphotypes identified (Table S1).
973 About half of these taxa corresponded to diatoms. Smaller protists in 5-20 μm size fractions
974 from SRF and DCM layers were retrieved from Colin et al. (2017) and obtained by
975 environmental high content fluorescence microscopy (eHCFM).

976 The taxonomic classification of mesozooplankton collected with nets was performed on
977 formaldehyde fixed samples scanned with the ZooScan imaging system (Gorsky et al., 2010)
978 and identified with the help of an automatic recognition algorithm to the deepest possible
979 taxonomic level using Ecotaxa (Picheral et al., 2017). The resulting identifications were
980 validated by specialists, and reached different taxonomic levels, mostly the family level (or
981 genus in some cases, e.g., copepods from the WP2 net). All images are accessible within
982 Ecotaxa (<http://ecotaxa.obs-vlfr.fr>). Mesozooplankton absolute abundances were calculated by
983 taking into account the volume of water filtered by the nets. Together with images, various
984 morphological measurements were obtained (also accessible within Ecotaxa). Major and
985 minor best ellipsoidal axis were used to calculate the ellipsoidal biovolume of each organism
986 that was used as a proxy of biomass. All other morphological measurements (such as length,
987 elongation, grey level values and distribution; except those related to position of organisms
988 within the initial scan) were recovered, normalized and used in a t-SNE analysis (van der
989 Maaten and Hinton, 2008) using MatLab software using the default settings (Euclidean
990 distances; Barnes-Hut algorithm; perplexity of 30; exaggeration of 4; learning rate of 500).
991 Different combinations of parameters were tested without clear improvements to the final
992 result shown in Figure 2B for the bongo net. t-SNE results were used to overlay taxonomic
993 information on the morphological overview of the imaging data sets.

994 Summary statistics of our datasets and their taxonomic resolution are provided in Table S1.
995 Based on their taxonomic affiliation, we classified all taxa into marine plankton groups
996 (MPGs) following the criteria indicated in Table S2. We did so not only to separate organisms
997 of different broad functions, but also to minimize biases that could arise when comparing
998 organisms with contrasting body size or marker gene copy number per organism (see below).
999 For viruses we considered the three families mentioned above separately as they are the most
1000 abundant groups and have different ecologies (Brum et al., 2015; Hingamp et al., 2013; Roux
1001 et al., 2016). For prokaryotes, we distinguished photosynthetic bacteria (i.e., cyanobacteria)
1002 from heterotrophic/chemotrophic bacteria and archaea. For protists, we used an extended
1003 version of the functional database used in de Vargas et al. (2015), which encompasses a wide
1004 variety of protist taxa that are assigned to major functional groups:
1005 photosynthetic/mixotrophic protists, endophotosymbionts, hosts with endophotosymbionts
1006 (hereafter photohosts), parasitic protists, and free-living heterotrophs or phagotrophs
1007 (hereafter heterotrophic protists). Note that the endophotosymbiont group is probably the
1008 most incomplete due to the difficulties in currently being able to define comprehensively
1009 these organisms. For the mesozooplankton, the categories used corresponded to the most
1010 abundant taxonomic groups (such as copepods and chaetognaths) or feeding strategies (Figure
1011 S2). We here only considered MPGs for which the total relative abundance in the molecular

1012 data set was > 1%, a threshold under which we considered that the detection level was too low
1013 to obtain reliable detection and diversity estimates. In total, we thus studied the diversity of 12
1014 MPGs, of which a full list is provided in Table S2.

1015 Plankton diversity was estimated at each station with the Shannon diversity index, a robust
1016 measure of entropy. We chose this index rather than richness because, unlike richness, the
1017 Shannon index is insensitive to sampling effort, provided that the sampling is not too shallow
1018 (Jost, 2006). As such, the sampling effort in our datasets – albeit very deep – varied across
1019 samples but the rarefaction curves drawn with the Shannon index were largely saturating
1020 contrary to those based on richness (Figure S3). The Shannon index has also been shown to
1021 provide more reliable diversity estimates when using DNA-based data (Bálint et al., 2018;
1022 Haegeman et al., 2013). Finally, by construction, it also relates monotonically with species
1023 richness, and should therefore exhibit similar patterns (Jost, 2006). The Shannon index was
1024 calculated separately for each MPG using the samples filtered at <0.22 μm , 0.22-3 μm and
1025 0.8-2000 μm for prokaryotic viruses, bacteria/giruses (metagenomics) and eukaryotic
1026 plankton (DNA metabarcoding), respectively. We also calculated the Shannon index for the
1027 full local planktonic communities (i.e., not parsed into MPGs) for each sampling protocol
1028 (i.e., metagenomics, metabarcoding, and imaging for each sampling mesh size). To ensure that
1029 our Shannon values were robust, we computed their variation from 100 Monte Carlo
1030 simulated communities (function EntropyCI, R-package 'entropart' v1.6-1, [https://cran.r-](https://cran.r-project.org/web/packages/entropart/)
1031 [project.org/web/packages/entropart/](https://cran.r-project.org/web/packages/entropart/); evaluated only for the eukaryotic plankton). Each
1032 variation range was very narrow and seldom overlap with the rest (difference between
1033 Shannon values from simulated communities, 0.003 ± 0.003 ; difference between Shannon
1034 values from samples; 0.969 ± 0.700), making this uncertainty negligible as compared to that
1035 generated by our downstream analyses. Shannon diversity for each MPG retrieved from
1036 microscopy/imaging data was in general not assessed due to low taxonomic resolutions, with
1037 the exception of microphytoplankton/diatoms identified with light microscopy, and the
1038 copepods collected with the WP2 net due to their relatively high taxonomic resolution (Figure
1039 S6), as explained above.

1040 Raw reads of *Tara* Oceans are deposited at the European Nucleotide Archive (ENA) under the
1041 number PRJEB9737. Imaging datasets from the nets are available through the collaborative
1042 web application and repository EcoTaxa (Picheral et al., 2017) under the address
1043 [http://ecotaxa.obs-](http://ecotaxa.obs-vlfr.fr/prj/412)
1044 [vlfr.fr/prj/397](http://ecotaxa.obs-vlfr.fr/prj/397), <http://ecotaxa.obs-vlfr.fr/prj/398>, <http://ecotaxa.obs-vlfr.fr/prj/395> for bongo
1045 data, and within the 2 projects <https://ecotaxa.obs-vlfr.fr/prj/377> and [https://ecotaxa.obs-](https://ecotaxa.obs-vlfr.fr/prj/378)
1046 [vlfr.fr/prj/378](https://ecotaxa.obs-vlfr.fr/prj/378) for WP2 data. A table with multiple samples identifiers and Shannon values is
1047 available as supporting material (see table of Data and Resources).

1048 Because every method to assess biodiversity has limitations, either due to technical issues
1049 (e.g., sampling difficulties, taxonomic resolution, lack of morphological/genetic differences)
1050 or more fundamentally due to the difficulties of classifying the diversity of life, we also
1051 assessed the congruence of diversity trends across methodologies to ensure the reliability of

1052 our conclusions. We therefore provide in Figure S6 several correlation analyses of the
1053 diversity patterns observed with a wide array of methodologies used in *Tara* Oceans, using
1054 previously published or newly released datasets. These comparisons include DNA-based
1055 diversity trends obtained with different markers, taxonomic resolution, and size fractions, as
1056 well as diversity trends obtained with different optical methods. More specifically, we
1057 compared the diversity trends for (a) different DNA markers (V9 vs V4 region of the 18S
1058 rRNA gene), (b) different taxonomic resolutions using different clustering similarity
1059 thresholds, and (c) molecular vs. optical approaches (the latter based both on abundance or
1060 biovolume). More details about the data sets are available in the legend of Figure S6.
1061 Additionally, we evaluated the potential effect of marker gene copy number in prokaryotes by
1062 correcting for gene copy numbers of the 16S rRNA gene. The correction was performed using
1063 copy number estimates of references in the SILVA database (v136; Louca et al., 2018), from
1064 which we could assign a 16S rRNA gene copy number value for almost all miTags in our
1065 dataset (99%). After the correction, Shannon values remained essentially unchanged
1066 (Pearson's r correlation between corrected and uncorrected Shannon values = 0.99, $p \ll$
1067 0.001). Furthermore, we relied on the strong correlation we showed in a previous study
1068 between Shannon values for bacterial OTUs defined either by 16S rRNA gene or by single-
1069 copy genes (Milanese et al., 2019).

1070

1071 **Latitudinal diversity gradient**

1072 Our first objective was to explore visually the LDG trend across all domains of life using both
1073 MOTU and morphotype diversity at each station. To this end, we used generalized additive
1074 models (GAMs, Hastie 2017) due to their ability to fit non-linear and/or non-monotonic
1075 functions which we expected between diversity and latitude. GAMs are further highly suitable
1076 for modeling large scale trends (Guisan et al. 2002). Additionally, we preferred the GAM
1077 smoothing approach over simple moving averages because priors are directly learned from the
1078 data and the sensitivity to extreme values is relatively low. For this particular analysis, GAMs
1079 were used only for visualizing the diversity trendline, and were not used in downstream
1080 analyses (see "Diversity modeling of MPGs"). Next, we analysed the shape of the LDG of
1081 each marine planktonic group in two ways. First, a segmented regression analysis was
1082 conducted to describe the form of the latitudinal gradient on absolute latitude. More
1083 specifically, we aimed at detecting latitudinal breakpoints and changes in slopes across
1084 latitude. For this we used the R package 'segmented' 0.5-3.0 ([https://cran.r-](https://cran.r-project.org/web/packages/segmented)
1085 [project.org/web/packages/segmented](https://cran.r-project.org/web/packages/segmented)). In order to determine which MPG displayed similar
1086 LDG forms, we computed pairwise Euclidean distances between the obtained set of latitudinal
1087 breakpoints and slope values for each MPG, and subjected the resulting distance matrix to a
1088 hierarchical clustering analysis (Figure S5). In an additional analysis, we further determined
1089 whether the LDG of each MPG exhibited a North-South asymmetry. To this end, we
1090 performed separate linear regressions for each hemisphere (Table S3).

1091

1092 **Diversity modeling of MPGs**

1093 Our second objective was to find predictors for local diversity of marine planktonic groups.
1094 To this end, we also used GAMs (see “Latitudinal diversity gradient” for description and
1095 references). All GAMs were built using the R library ‘mgcv’ 1.8-24 ([https://cran.r-](https://cran.r-project.org/web/packages/mgcv/)
1096 [project.org/web/packages/mgcv/](https://cran.r-project.org/web/packages/mgcv/)), using only MOTU diversity of each MPG as response
1097 variable. Smooth terms (‘s’) were based on a thin plate regression splines and estimated by a
1098 Laplace approximation marginal likelihood criterion (Wood, 2010). The rest of the parameters
1099 were set on default mode.

1100 In order to test the different hypotheses explaining plankton latitudinal diversity gradients and
1101 patterns of diversity in general, we first made a selection of variables from the *Tara* Oceans
1102 contextual data and public databases (see “Physical and environmental measurements”) that
1103 relate to these hypotheses and/or that were sufficiently available across our global sampling.
1104 We then evaluated their redundancy and their link with MPG diversity by conducting multiple
1105 pairwise correlation analyses with the Spearman rank correlation test (Figure 3A, S8). We
1106 considered the contextual variables associations having $|\text{Spearman's } \rho| > 0.6$ to be highly
1107 correlated and kept only the most representative and biologically meaningful variable
1108 amongst correlated ones to avoid collinearity in downstream analyses. We excluded null
1109 hypotheses for the LDG, such as the area (Willig et al., 2003) or mid-domain effect (Colwell
1110 and Lees, 2000) due to the high interconnectivity of the global ocean, which should limit the
1111 geometric constraints imposed on species distribution on lands.

1112 The associations of plankton diversity with the four selected contextual variables (i.e., SST,
1113 chlorophyll *a*, annual maximum of nitrate concentration, and intra-annual variation of SST)
1114 were further analysed using GAMs, as we expected them to be non-linear or non-monotonic
1115 functions based on previous studies (e.g. Tittensor et al., 2010; Vallina et al., 2014). Except
1116 for SST, the contextual variables were \log_{10} -transformed. For chl *a*, three low-concentration
1117 outlier values were excluded. “Individual” GAMs were built for each MPG and each
1118 contextual parameter, from which the explained deviance was used as an association measure
1119 and the approximate p-value of the smooth term to account for effect significance. All p-
1120 values obtained were corrected for multiple comparisons (Holm, 1979). To further test the
1121 different LDG hypotheses, we then built “full” GAMs for each MPG that included all four
1122 contextual variables, with the settings explained above. Their additive contribution was
1123 calculated by a sequential removal of the different parameters and a normalization with a null
1124 model.

1125 From these analyses, we identified temperature and chlorophyll *a* to be the best correlates
1126 with most MPGs diversity. These two variables also capture relatively well other
1127 environmental gradients, such as cyanobacteria and mesozooplankton abundance (Figure 3).
1128 Given their strong explanatory power and because their current and future state at the sea
1129 surface can be simulated with global ocean circulation models (Bopp et al., 2013), we used
1130 them to predict the current global-scale distribution of MPGs diversity, as well as its response
1131 to a severe scenario of climate and oceanic change. To this end, we built a set of “reduced”

1132 GAMs with surface diversity for each MPG as response variable, and SST, chlorophyll *a*, as
1133 well as an interaction-like term (included as a tensor product, ‘*ti*’), as explanatory variables.
1134 SST and chlorophyll *a* (*in situ* measurements) were only partially anti-correlated, probably
1135 due to a decoupling in upwelling systems (Demarcq, 2009). Accordingly, the explained
1136 deviance of some of our GAMs was increased by 10% or more when considering these two
1137 parameters without affecting their parsimony.

1138 Both “full” and “reduced” GAMs were built with the same approaches as described above and
1139 were further validated with two additional analyses. First, we quantified the congruence
1140 between observed and GAM-modeled Shannon diversity values through a Pearson’s
1141 correlation analysis. Second, we ensured that the GAM residuals did not exhibit latitudinal or
1142 longitudinal trends, a way to control for spatial autocorrelation (Tables S5 and S7). Checking
1143 the absence of latitudinal trends in the model residuals further indicates if our models
1144 successfully explained the latitudinal gradients of diversity. To further assess the performance
1145 of the “reduced” models used downstream for predicting current and future trends of
1146 diversity, we cross-validated them with other independently collected molecular datasets from
1147 open-ocean studies targeting either heterotrophic bacteria (Zinger et al., 2011) or the whole
1148 planktonic eukaryotic community (Raes et al., 2018) from different sampling dates and
1149 locations. Splitting this latter dataset into MPGs was not possible due to the unavailability of
1150 functional databases for the DNA marker used (V4 region of the 18S rRNA gene), so we
1151 conducted this cross-validation with a reduced GAM model built for the whole eukaryotic
1152 community. Figure S13 shows that the GAM models built with our datasets are able to predict
1153 correctly the diversity trends of plankton communities observed in these independent datasets
1154 (see complementary details in the caption of Figure S13 and below for CMIP5 models).
1155 Additionally, as both datasets include sampling points in the Southern Ocean, which was
1156 undersampled in ours, this agreement confirms the decrease in plankton diversity we observed
1157 towards the south.

1158 Next, the MOTU diversity of the six MPGs for which “reduced” GAMs yielded a deviance
1159 explained $\geq 60\%$ was modelled for the beginning and the end of the 21st century. To do so, we
1160 first defined a coarse-grained arrange of 1° grid-cells. SST and chlorophyll *a* content across
1161 space and time were obtained from the Coupled Model Intercomparison Project Phase 5
1162 (CMIP5), a multi-model simulation of the ocean (Bopp et al., 2013). Each model within
1163 CMIP5 is an Earth system simulation generated by different research groups (Table S8),
1164 which allows us to account for different mechanistic weights. We extracted the two variables
1165 from each CMIP5 model for each grid cell for the beginning of the 21st century (averaged
1166 values for years 1996-2005) and the end of the 21st century (averaged values for years 2090-
1167 2099), the latter considering RCP 8.5 scenario, the most pessimistic IPCC trajectory for
1168 greenhouse gases concentration (radiative forcing level reaches 8.5 W/m^2). To obtain an
1169 average and assess the uncertainty in our predictions, we generated a combined calculation of
1170 the uncertainty of the GAM parameters and the multiple CMIP5 models. We did so by first
1171 obtaining posterior distributions of the fitted GAM parameters for the different plankton
1172 groups. We then sampled values from these distributions randomly to generate 1,000 models.

1173 For each of these models, we used each of the CMIP5 models (n = 13) as current and future
 1174 temperatures and chl *a*. Shannon diversity was then predicted with each of the 13,000 models
 1175 we generated for each MPG and each time of projection (beginning and the end of the
 1176 century), from which we assessed the uncertainty of our predictions.

1177 Anomalies between future ocean projections and estimates for the beginning of the 21st
 1178 century were calculated as the difference between the average diversity of each planktonic
 1179 group projected for the time interval 2090-2099 and the one for 1996-2005. In other words, a
 1180 positive anomaly means that the predicted diversity will increase towards the end of the
 1181 century. Confidence intervals of anomalies were based on the standard deviations of the
 1182 average Shannon diversity estimates across the different CMIP5 models. Finally, to assess
 1183 potential areas in the future ocean where the effect of primary production change on diversity
 1184 could override the effect of temperature, we performed diversity projections holding either
 1185 SST or chlorophyll *a* constant, and then comparing their output. That is, we assessed per grid-
 1186 cell whether the effect of chlorophyll *a* on diversity was significantly larger than zero and
 1187 larger than the one of SST (in absolute values; see Figure 12D). Manipulation and
 1188 visualization of the CMIP5 spatial data and the corresponding diversity projections were
 1189 performed combining R packages ‘ncdf4’ 1.16 ([https://cran.r-](https://cran.r-project.org/web/packages/ncdf4)
 1190 [project.org/web/packages/ncdf4](https://cran.r-project.org/web/packages/ncdf4)), ‘raster’ 2.5-8 ([https://cran.r-](https://cran.r-project.org/web/packages/raster)
 1191 [project.org/web/packages/raster](https://cran.r-project.org/web/packages/raster)) and ‘rasterVis’ 0.43 ([https://cran.r-](https://cran.r-project.org/web/packages/rasterVis)
 1192 [project.org/web/packages/rasterVis](https://cran.r-project.org/web/packages/rasterVis)).

1193

1194 **Comparison of future trends with current areas of high socioeconomic and conservation**
 1195 **value**

1196 We identified the latitudes that are expected to experience the most dramatic changes in
 1197 diversity (defined as the 25% of latitudes with the highest mean absolute diversity anomalies)
 1198 and analysed whether these areas overlap with current ecosystem services and reserves. To
 1199 this end, we compared their corresponding current status in terms of (i) carbon export, using
 1200 satellite-derived estimates at 100 m depth (Henson et al., 2012), (ii) maximum marine
 1201 fisheries catch between years 2010-2014 (Watson, 2017), and (iii) number of marine protected
 1202 areas (Bruno et al., 2018) relative to the global average. In all cases, the difference was
 1203 expressed as the relative (%) increase or decrease in relation to the global average (Table S9).

1204

Data deposited and resource data		
18S rRNA gene metabarcoding (<i>Tara Oceans</i>)	de Vargas et al., 2015; this paper	European Nucleotide Archive (ENA) - PRJEB9737
OM-RGCv2 (<i>Tara Oceans</i>)	Salazar et al., in press	European Nucleotide Archive (ENA) - See their Table S1 for details

GOV 2.0 (<i>Tara Oceans</i>)	Gregory et al., 2019	European Nucleotide Archive (ENA) - See their Table S3 for details
ZooScan imaging - regent net, 680 μm (<i>Tara Oceans</i>)	This paper	EcoTaxa, http://ecotaxa.obs-vlfr.fr/prj/412
ZooScan imaging - bongo net, 300 μm (<i>Tara Oceans</i>)	This paper	EcoTaxa, http://ecotaxa.obs-vlfr.fr/prj/397 , http://ecotaxa.obs-vlfr.fr/prj/398 , http://ecotaxa.obs-vlfr.fr/prj/395
ZooScan imaging - WP2 net, 200 μm (<i>Tara Oceans</i>)	This paper	EcoTaxa, https://ecotaxa.obs-vlfr.fr/prj/377 , https://ecotaxa.obs-vlfr.fr/prj/378
Contextual data (<i>Tara Oceans</i>)	Sunagawa et al., 2015; this paper	https://doi.org/10.1594/PANGAEA.875582
CMIP5 Earth system models	Bopp et al., 2013	See our Table S8 for details
Sample identifiers & Shannon values; flow cytometry abundances	This paper; Sunagawa et al., 2015	Mendeley Data, Temporary link: https://data.mendeley.com/datasets/p9r9wttjkm/draft?a=ab9b5a3d-0529-4b64-a202-6196d12f4200
Software and Algorithms		
R v.3.5.1	R Core Team 2018	https://www.r-project.org
R package mgcv 1.8-24	Wood 2015	https://cran.r-project.org/web/packages/mgcv/index.html
R package segmented 0.5-3.0		https://cran.r-project.org/web/packages/segmented/index.html

1205

1206 **Lead Contact and Materials Availability**

1207 Further information and requests for resources and reagents should be directed to and will be
1208 fulfilled by the Lead Contact, Chris Bowler (cbowler@biologie.ens.fr).

1209 **Supplementary information**

1210 See corresponding supplementary files.

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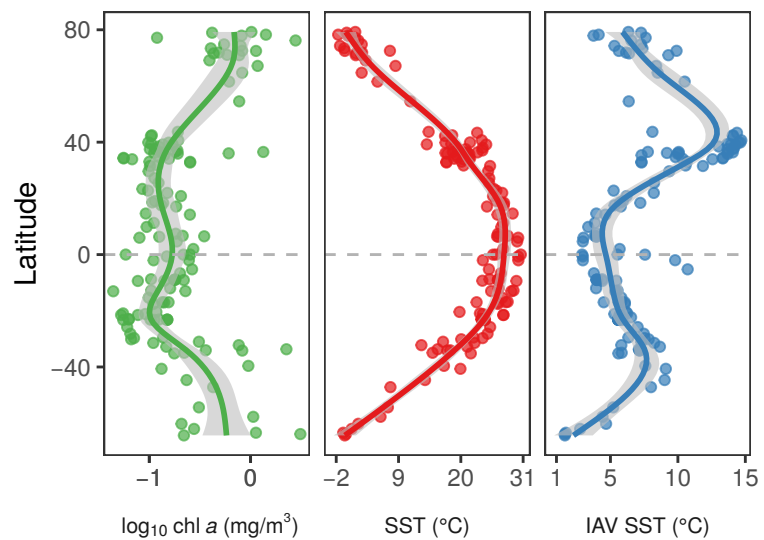
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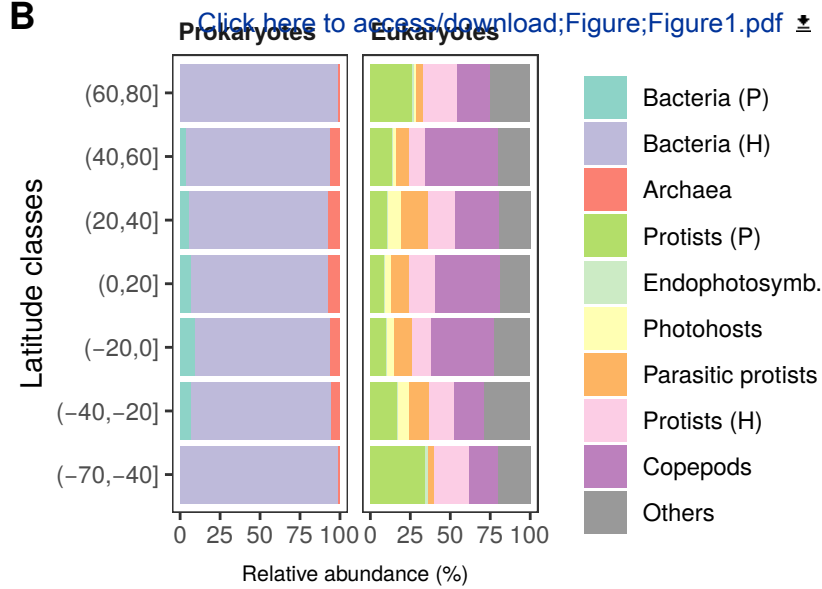
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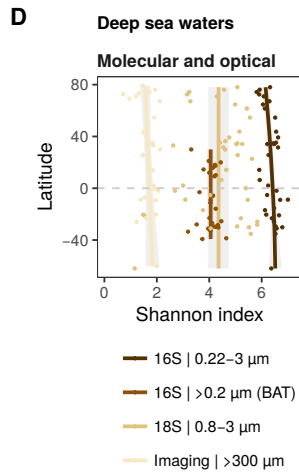
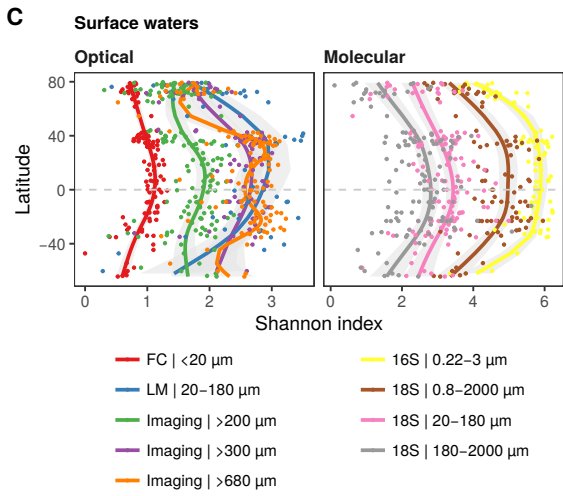
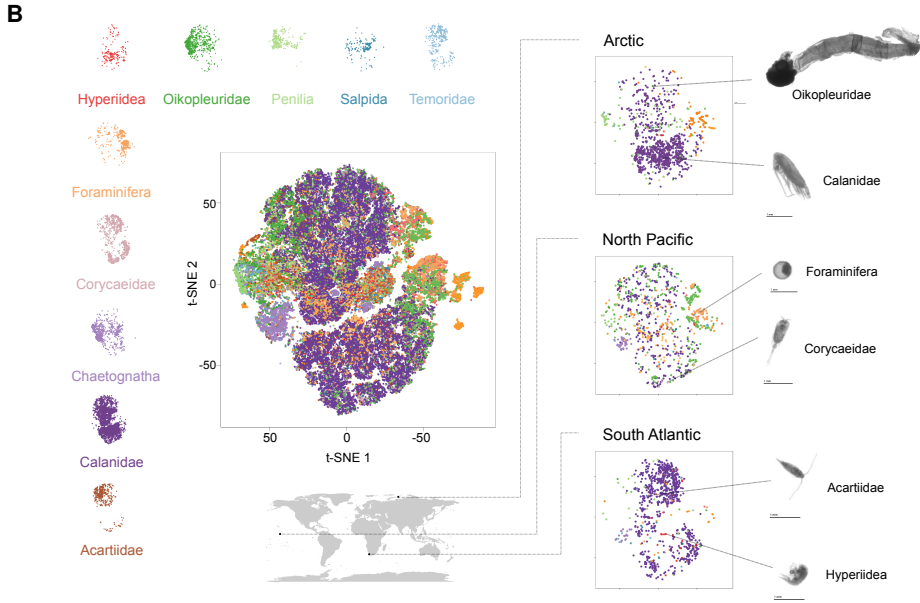
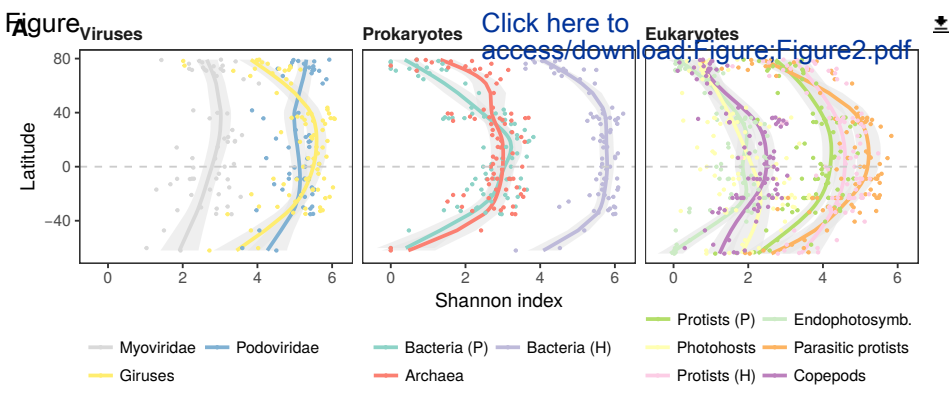
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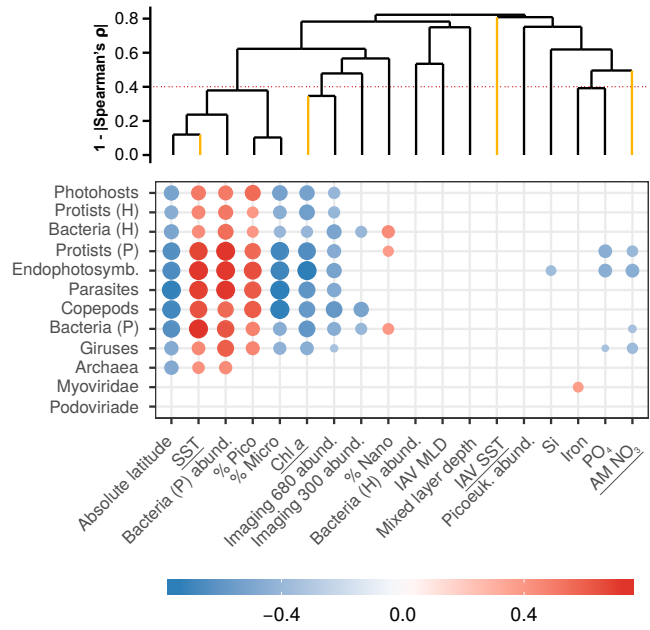


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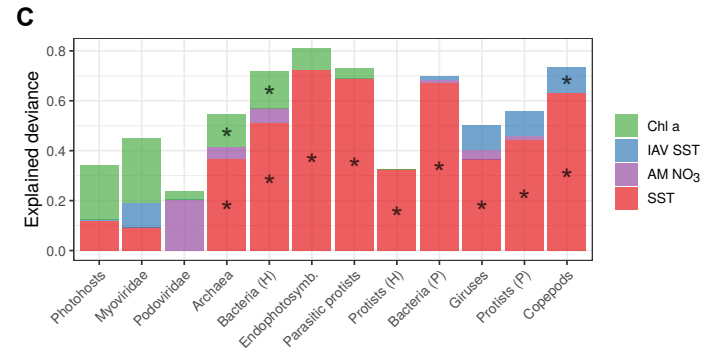
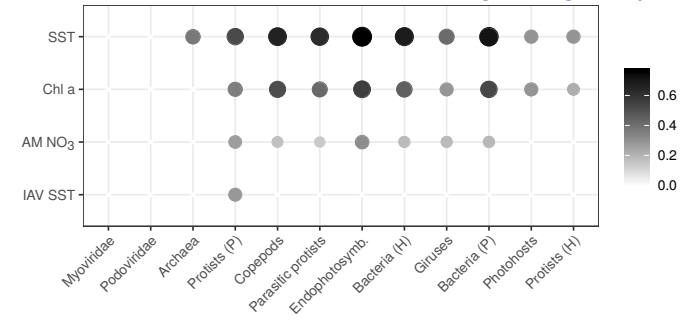


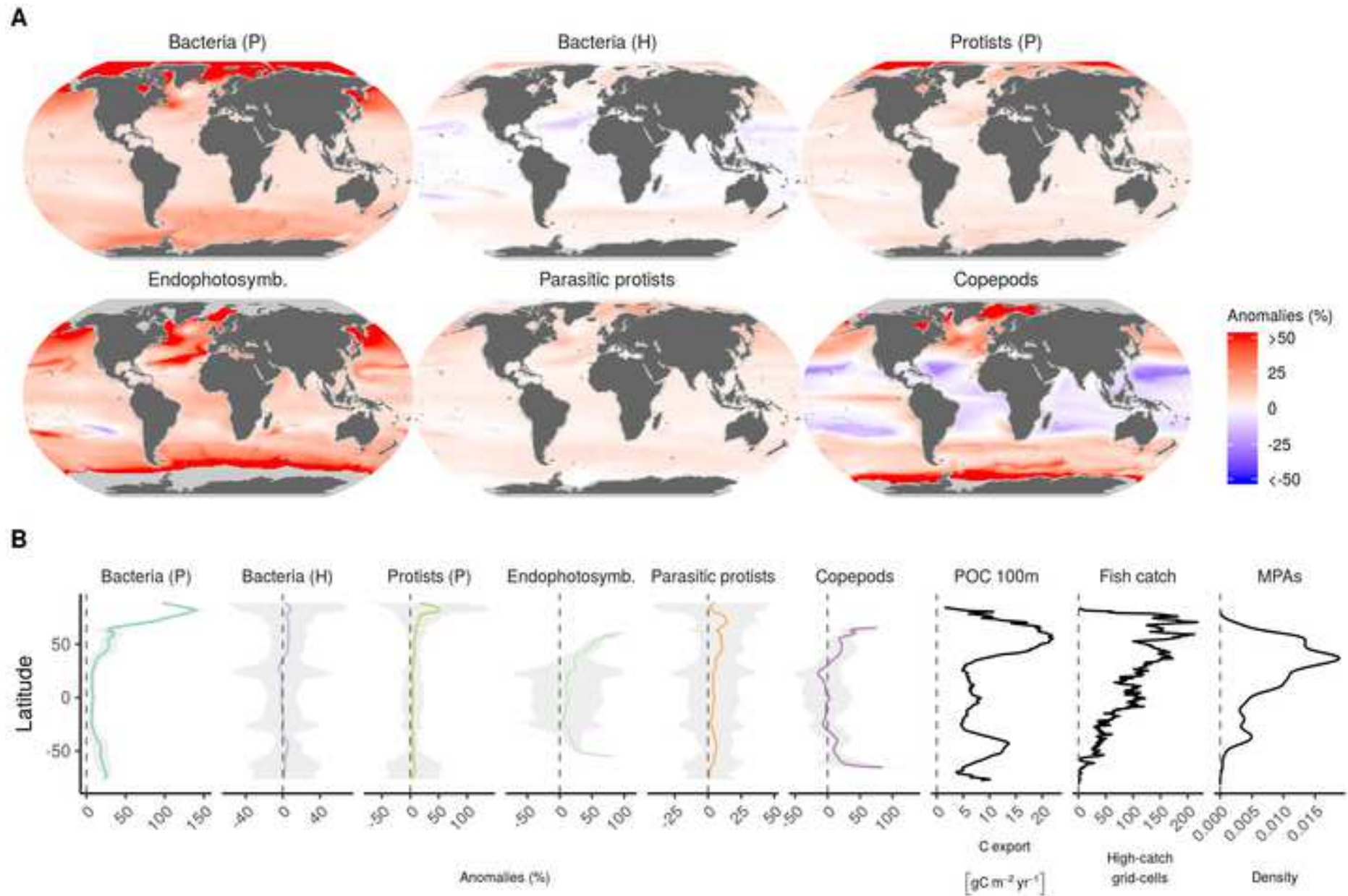


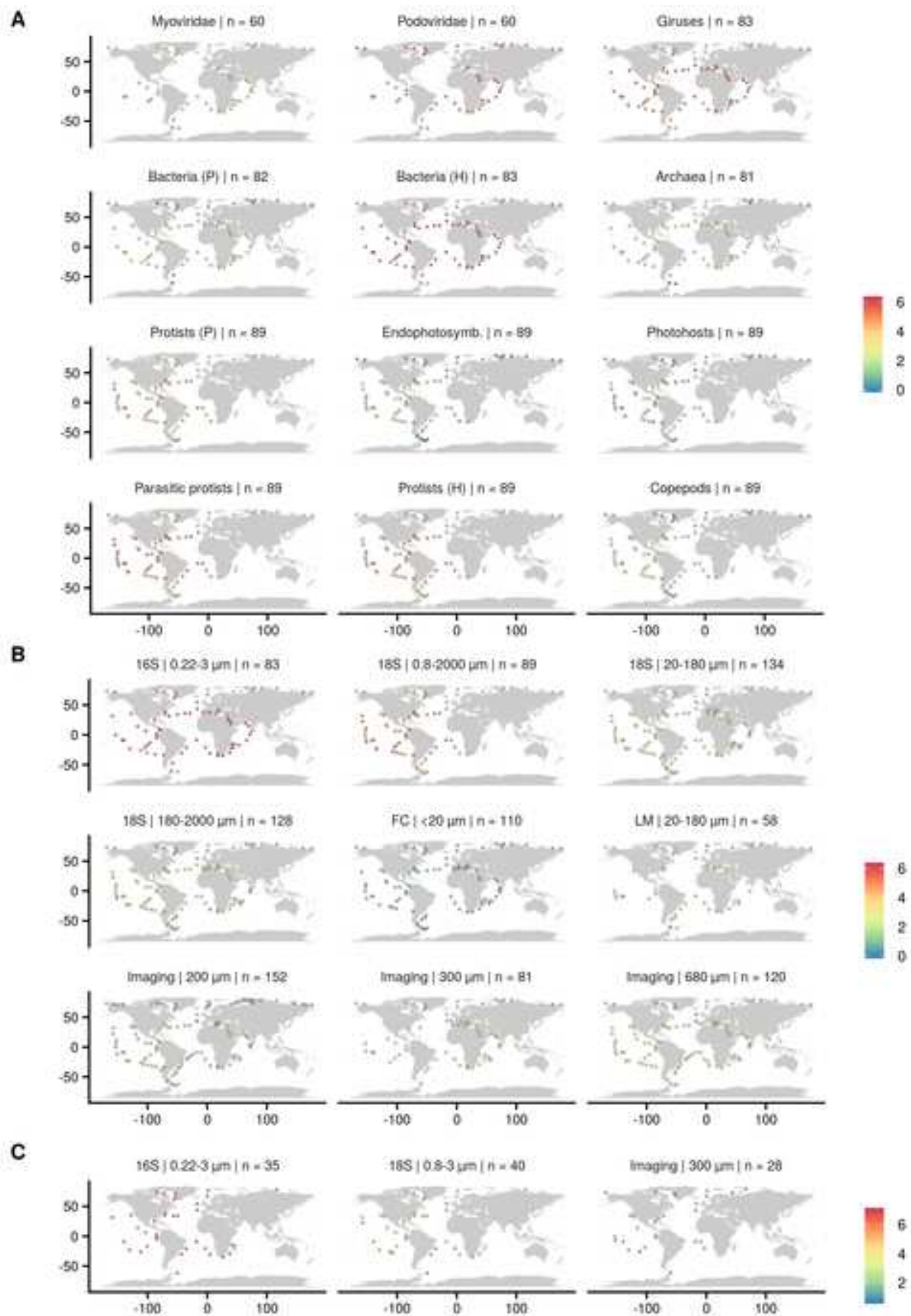
Figure



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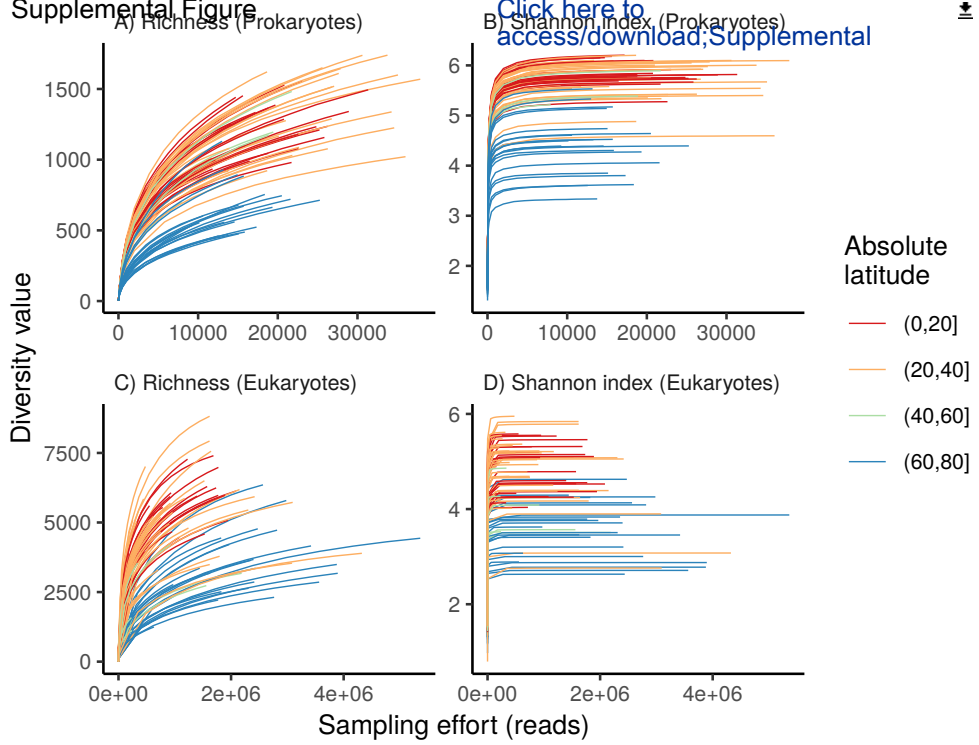


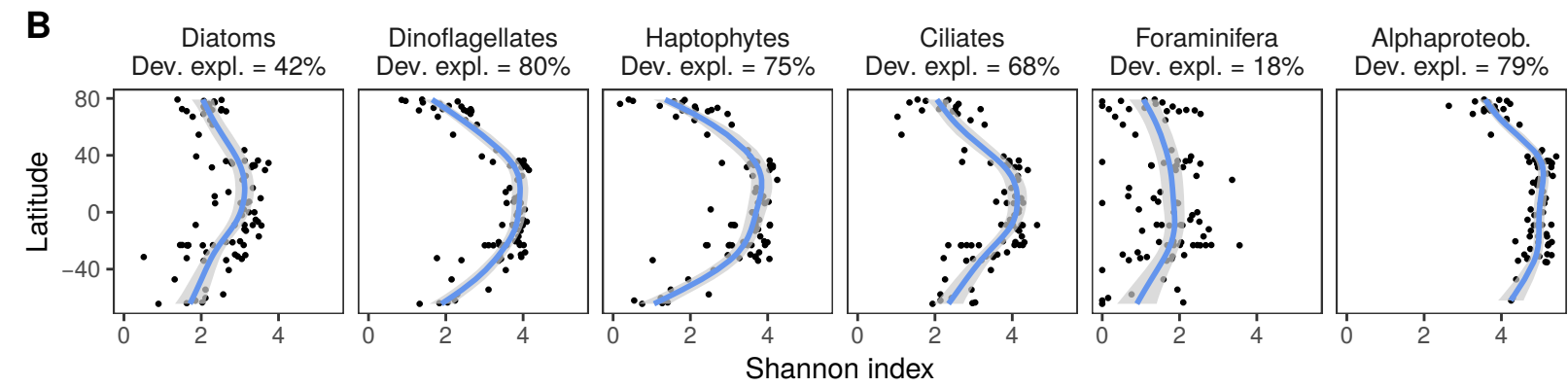
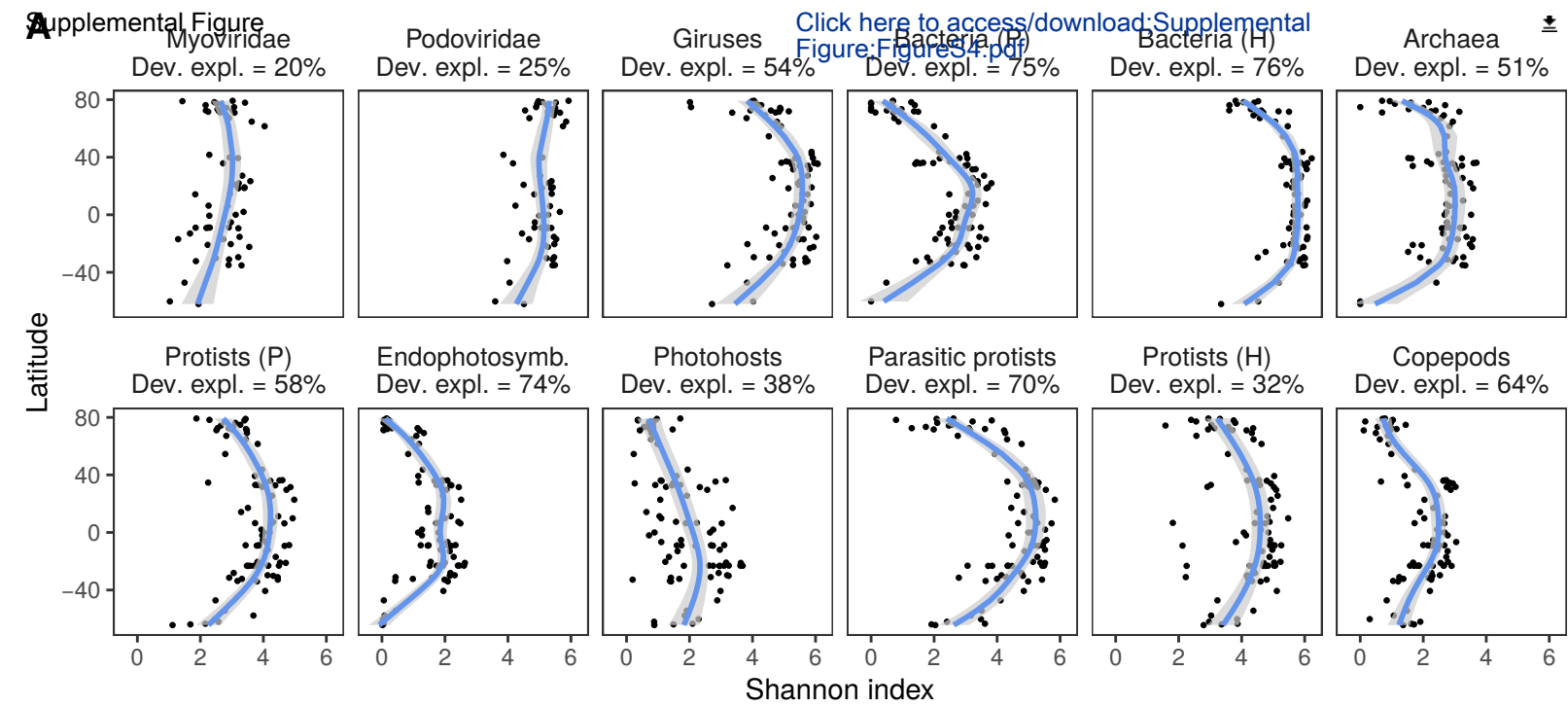


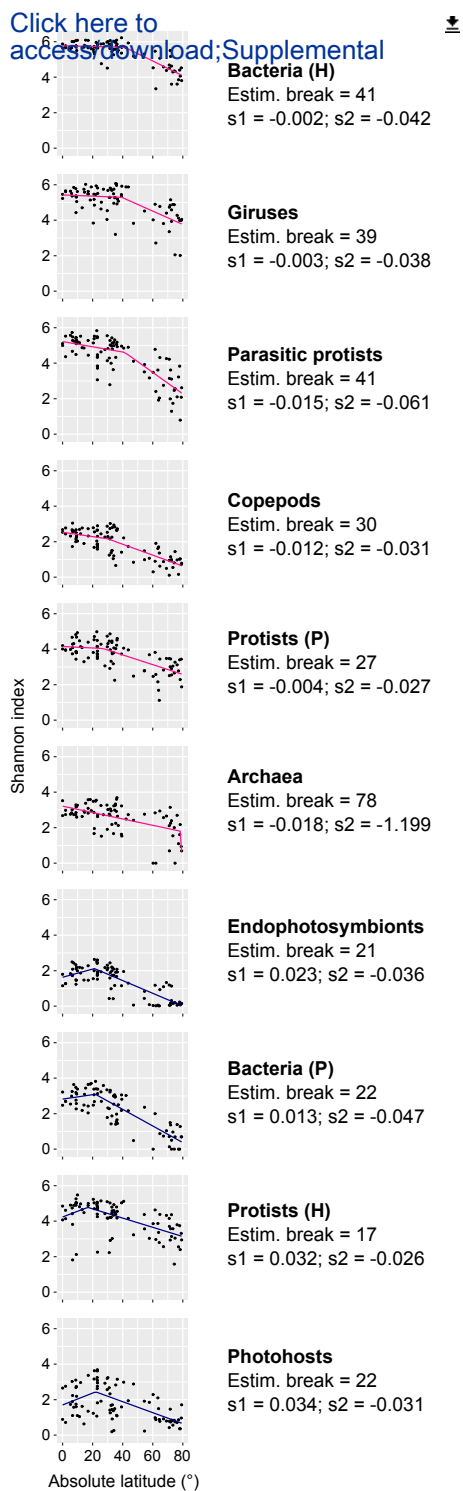
Supplemental Figure

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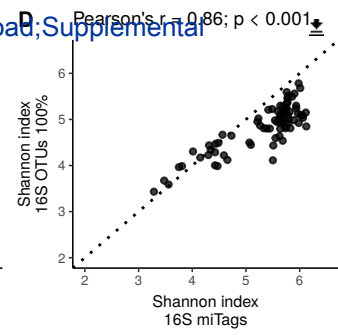
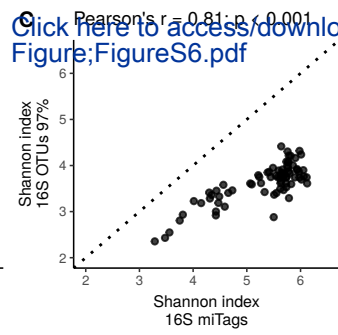
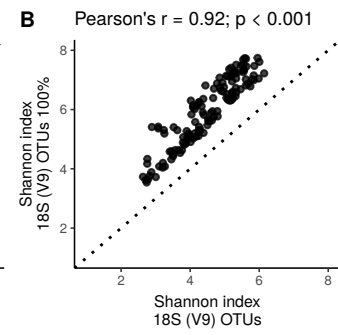
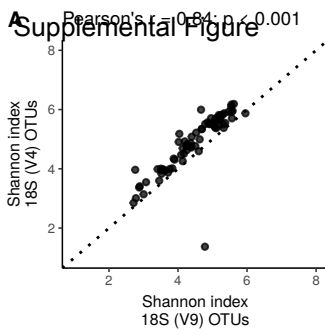




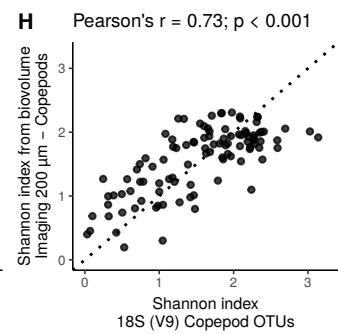
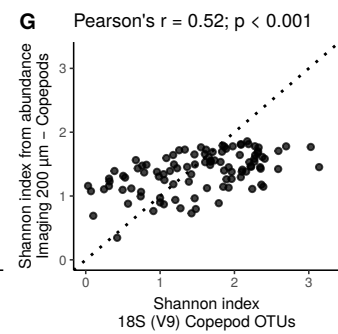
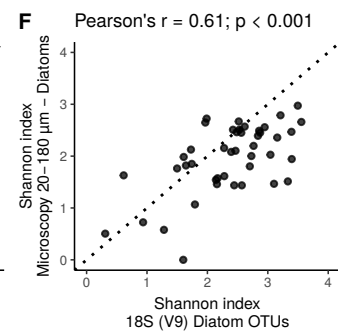
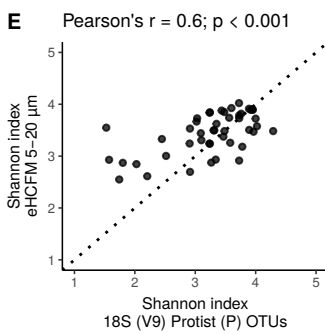




Supplemental Figure

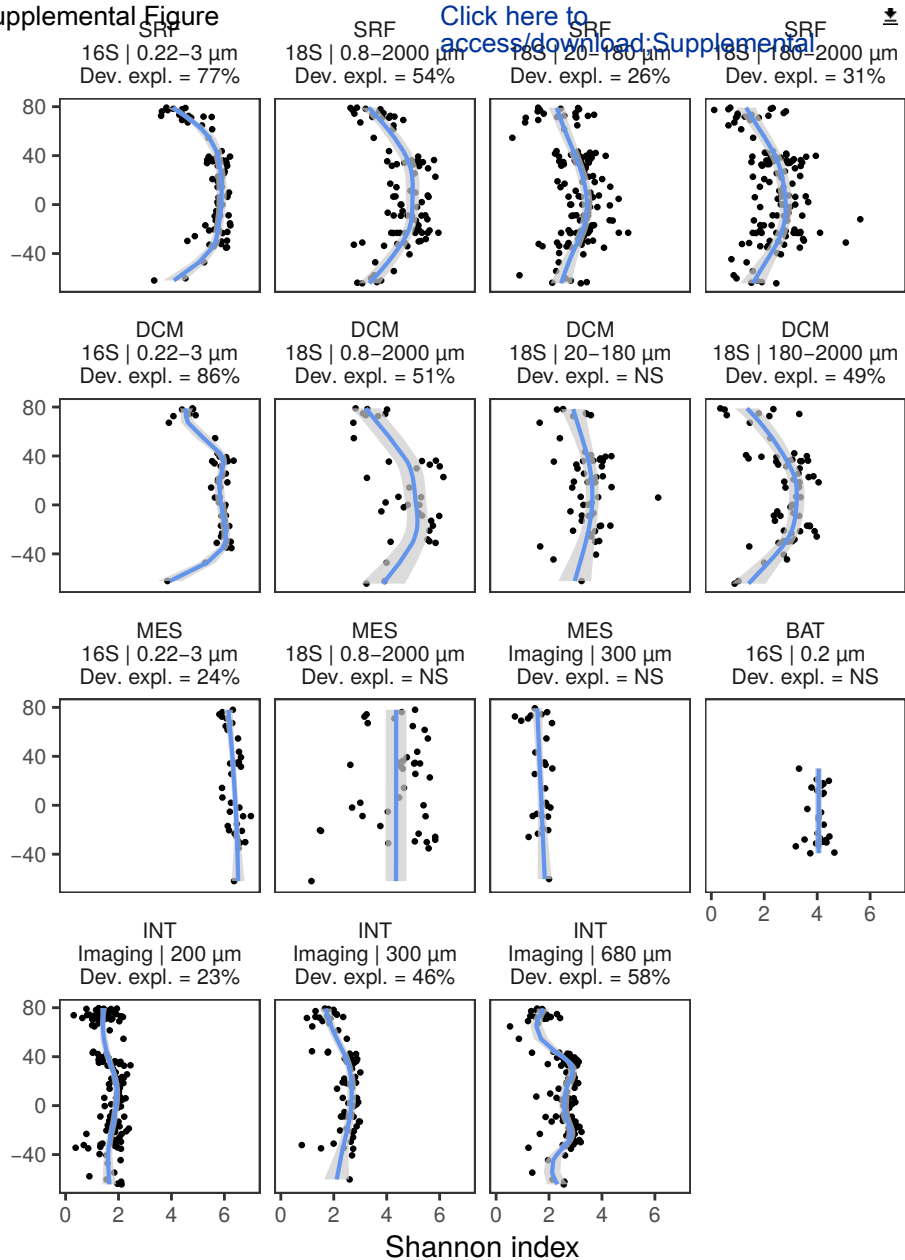


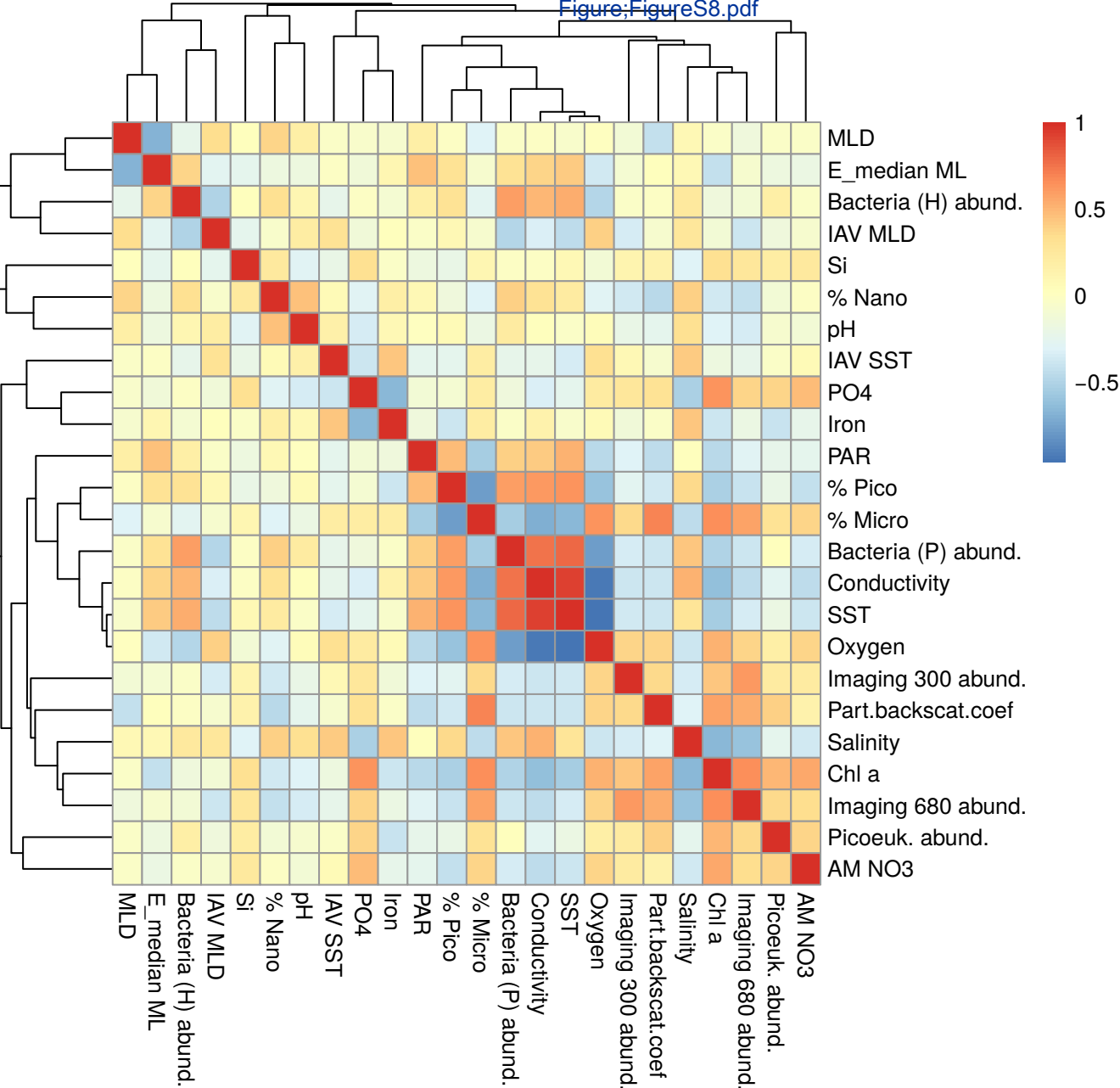
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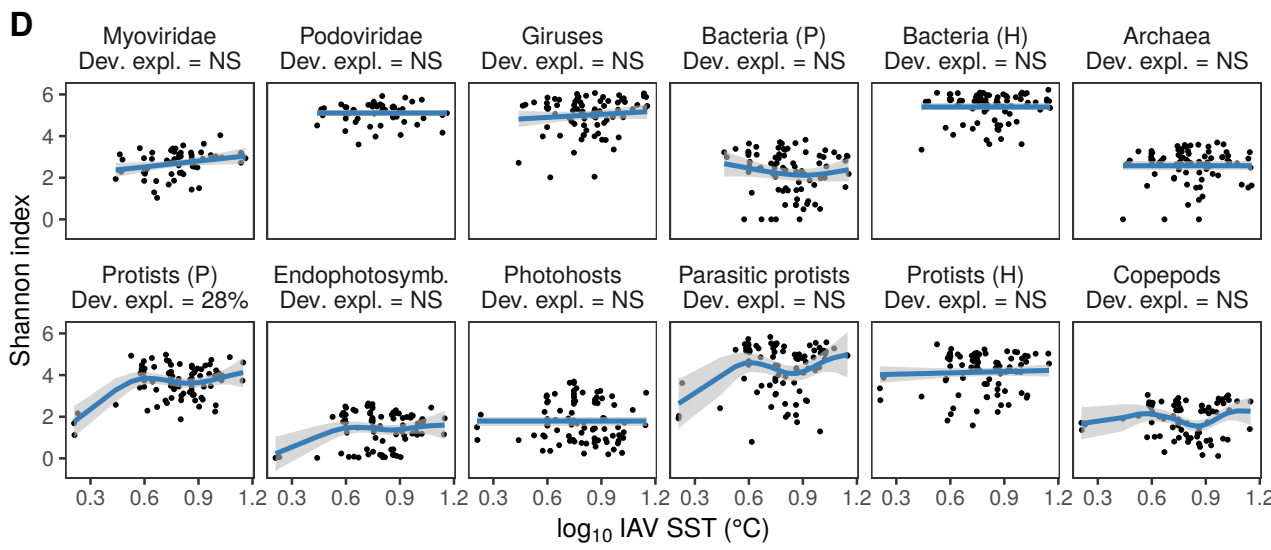
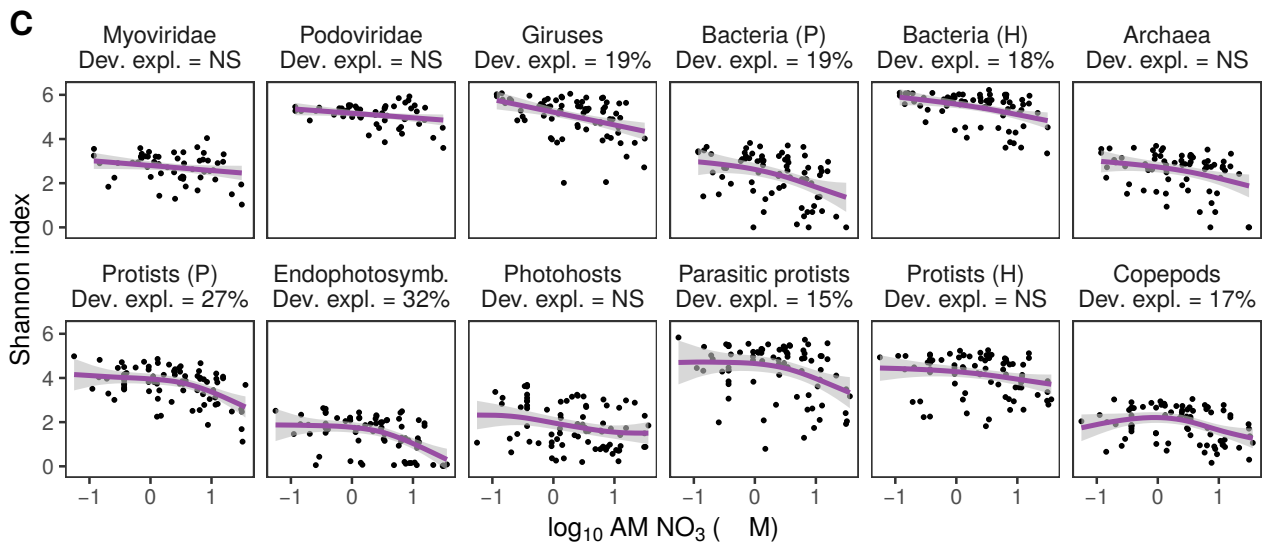
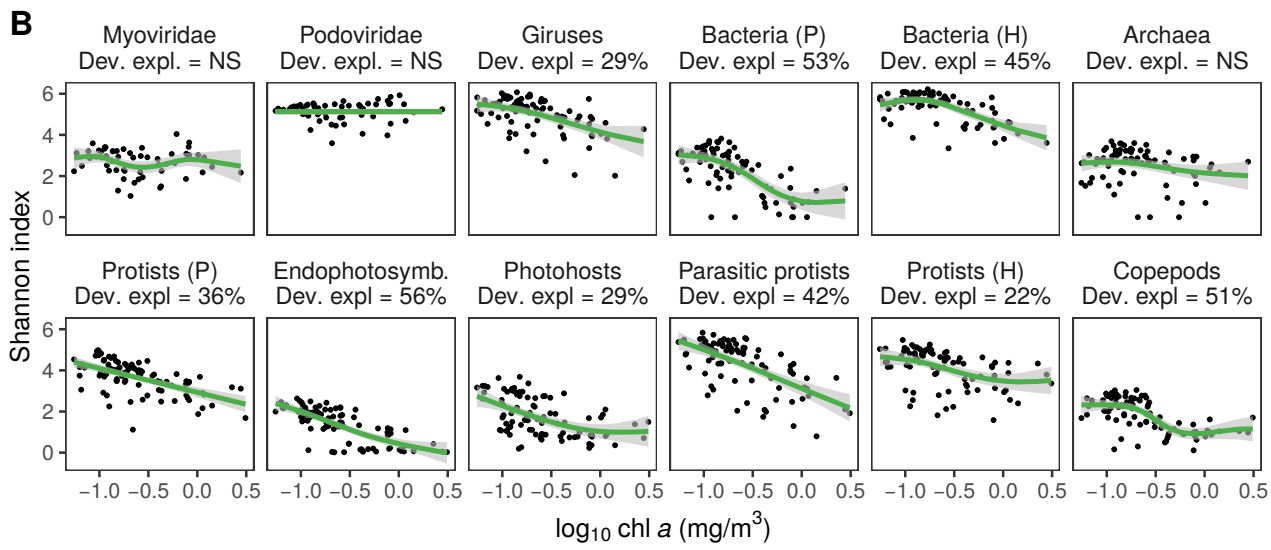
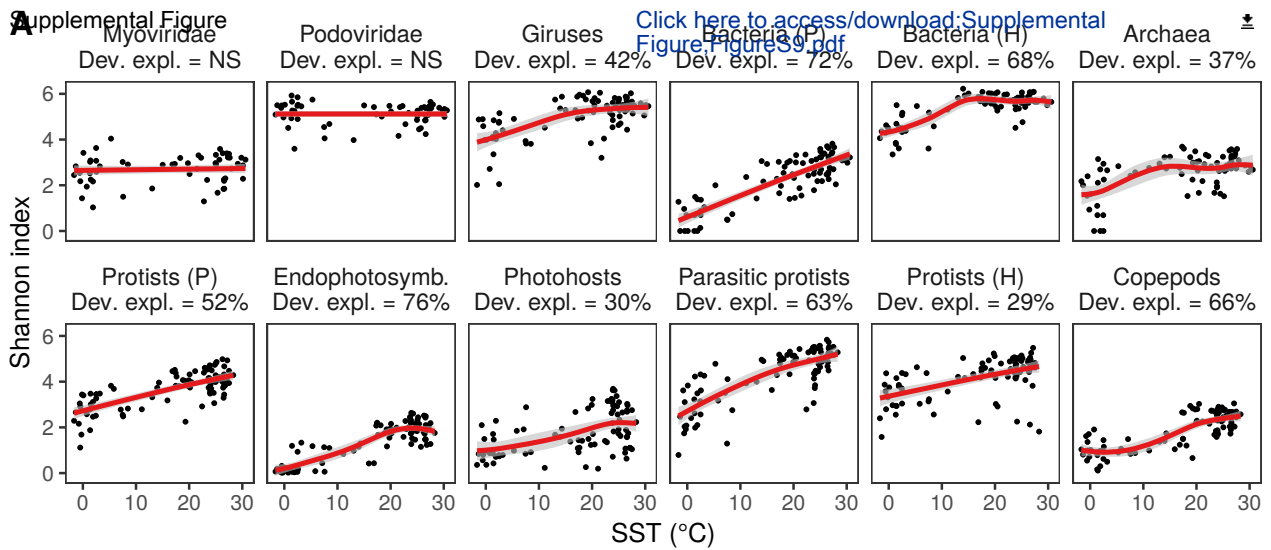


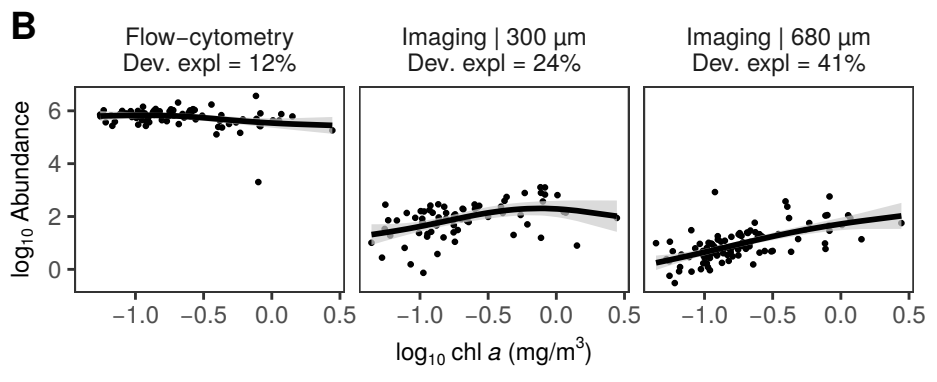
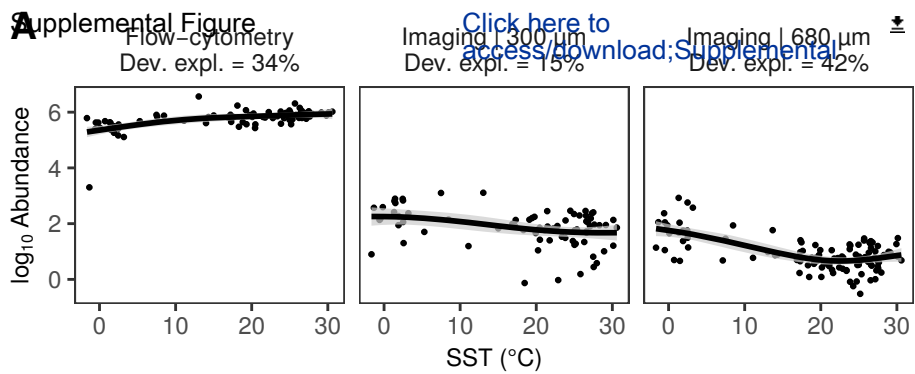
Supplemental Figure

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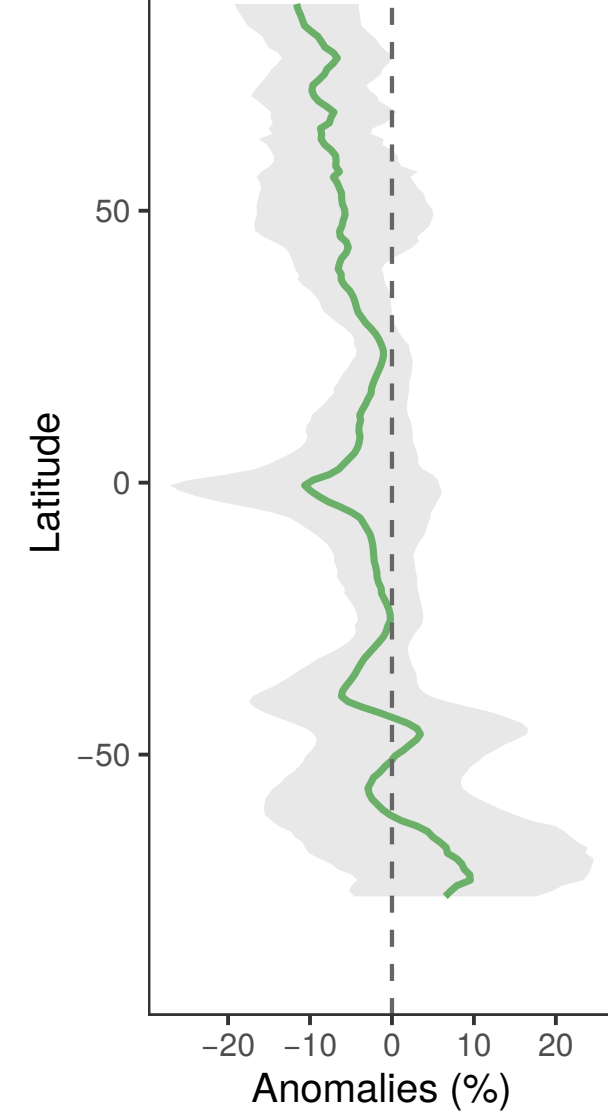
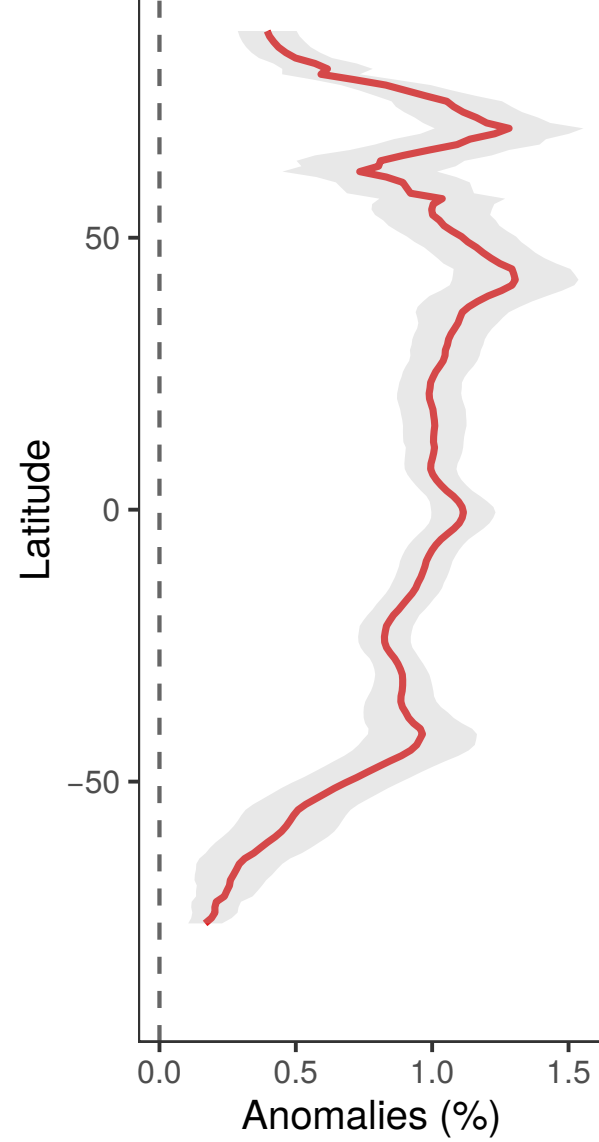


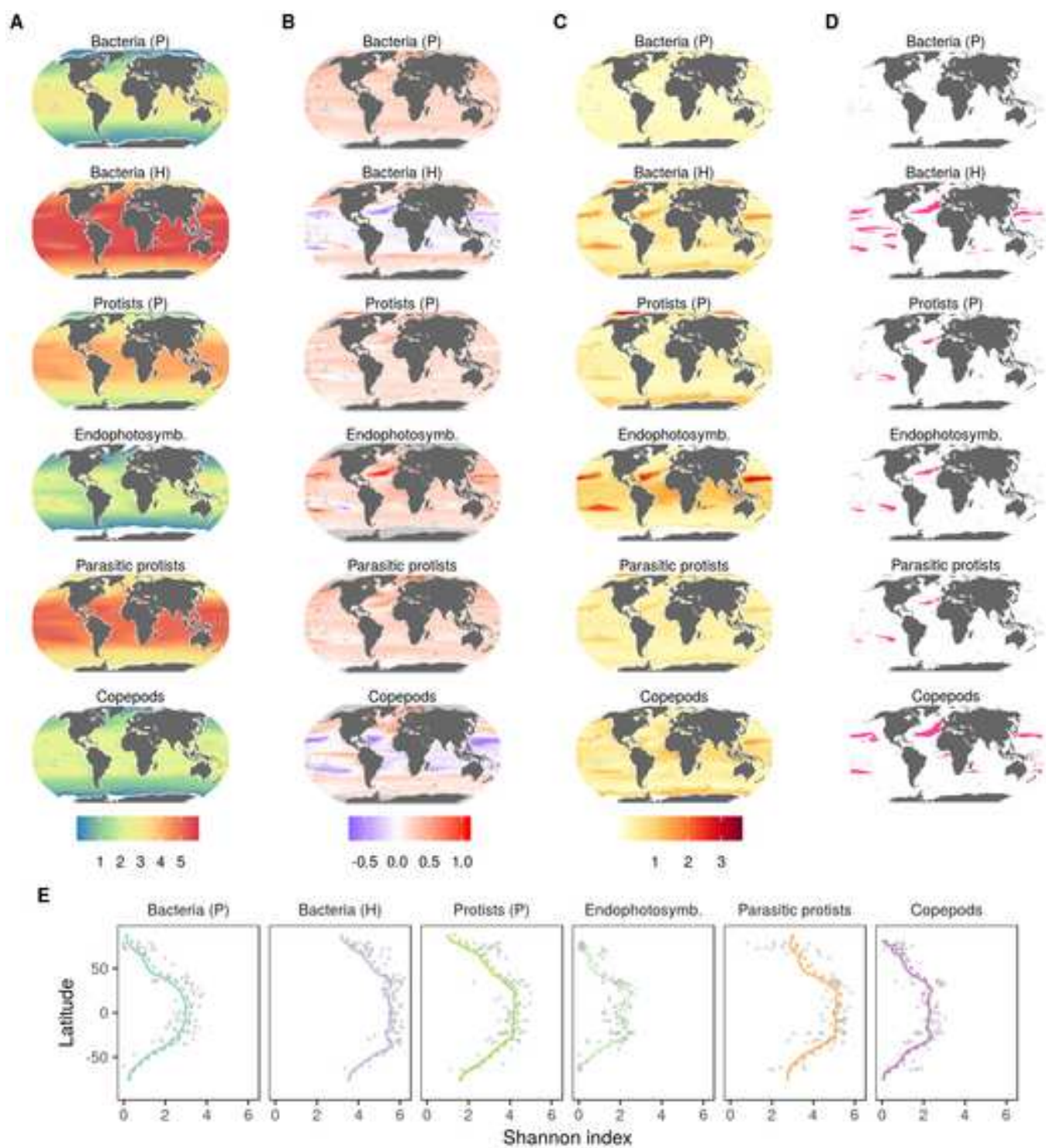




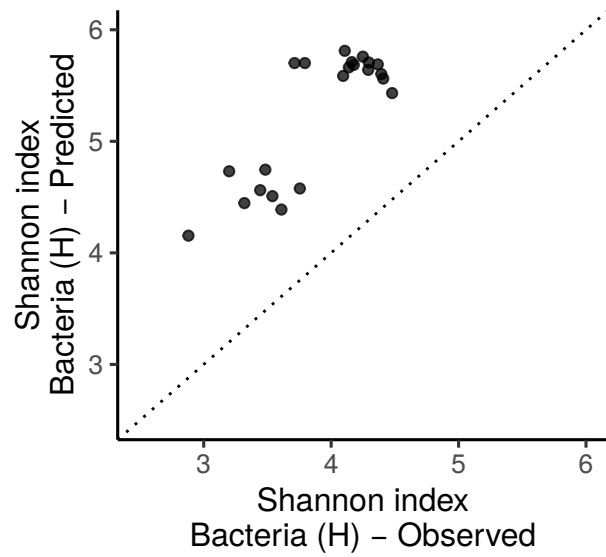


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A Supplemental Figure 1
Pearson's $r = 0.84$; $p < 0.001$



B Supplemental Figure 13
Pearson's $r = 0.45$; $p < 0.001$

