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Picoeukaryotes of the *Micromonas* genus: sentinels of a warming ocean

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Abstract

Photosynthetic picoeukaryotes in the genus Micromonas show among the widest latitudinal distributions on Earth, experiencing large thermal gradients from poles to tropics. Micromonas comprises at least four different species often found in sympatry. While such ubiquity might suggest a wide thermal niche, the temperature response of the different strains is still unexplored, leaving many questions as for their ecological success over such diverse ecosystems. Using combined experiments and theory, we characterize the thermal response of eleven Micromonas strains belonging to four

species. We demonstrate that the variety of specific responses to temperature in the Micromonas genus makes this environmental factor an ideal marker to describe its global distribution and diversity. We then propose a diversity model for the genus Micromonas, which proves to be representative of the whole phytoplankton diversity. This prominent primary producer is therefore a sentinel organism of phytoplankton diversity at the global scale. We use the diversity within Micromonas to anticipate the potential impact of global warming on oceanic phytoplankton. We develop a dynamic, adaptive model and ran forecast simulations, exploring a range of adaptation time scales, to probe the likely responses to climate change. Results stress how biodiversity erosion depends on the ability of organisms to adapt rapidly to temperature increase.

INTRODUCTION

1

2 The Intergovernmental Panel for Climate Change (IPCC) stressed unequivocal
3 warming of the climate system. Their Fifth Report anticipates rises in the global
4 mean surface temperature by the end of 21st century ranging from 0.3-1.7 °C
5 (RCP2.6) to 2.6-4.8 °C (RCP8.5) [1]. Oceans participate in buffering the increasing
6 emissions of greenhouse gases, thus modulating the warming; in addition to
7 the chemical equilibration of gas species between the atmosphere and dissolved
8 phases, phytoplankton is an important contributor of carbon remediation through
9 CO₂ sequestration in the ocean [2]. Should dramatic shifts occur in species biodi-
10 versity and distribution following temperature increases [3, 4], the resilience of
11 ecosystems could severely be impaired. The likely responses of ecosystems to such
12 rapid temperature changes are at the core of debates, with worrisome consequent
13 impacts on oceanic biogeochemical cycles and feedbacks on the climate system
14 [5].

15 Phytoplankton live in a thermally fluctuating environment that constrains growth
16 capacity [3, 6, 7]. The temperature growth response of phytoplankton varies
17 widely, both between and within taxa. Phenotypic plasticity determines the ability
18 to acclimate to short-term environmental variations while genetic adaptations
19 characterize evolutionary processes under long-term changes. These features
20 will provide, or not, each species with the capacity to survive in a given biotope
21 and to evolve by modifying their thermal niche. Since temperature depends on
22 latitude [8, 9, 10, 11], it is therefore a probable driver of niche partition in the
23 oceans, creating large-scale biogeographic patterns [12]. Hence, the structure and
24 diversity of phytoplankton communities could partly reflect observed trends in
25 the global temperature [6, 7].

26 Temperature-related interspecific distributions have been studied for the whole
27 phytoplankton community [3] but few studies explored intragenus diversity
28 [13, 14]. *Micromonas* species have emerged as emblematic representative of the

29 eukaryotic pico-phytoplankton communities, thriving in a variety of ecosystems
30 from polar to tropical waters [15, 16, 17, 18]. They often dominate phytoplankton
31 in coastal environments [19], where their major contribution to primary produc-
32 tion influences the biogeochemical cycles [20]. In the past decade, phylogenetic
33 analyses identified several distinct genetic lineages within *Micromonas* and have
34 suggested that this genus was composed of cryptic species [21, 22, 23, 24]. Four
35 species have now been formally described [25]. *Micromonas* spp. may co-occur at
36 various latitudes, but were found to occupy different temporal or depth niches
37 within their sympatric ranges [23].

38 As observed for picocyanobacteria [26, 13], the temperature response of such a
39 widely distributed and phylogenetically diverse eukaryote is expected to vary
40 between *Micromonas* species. The interspecific diversity within the genus *Mi-*
41 *cromonas*, the number of characterized strains, and abundant omics data make it a
42 relevant model organism to both explore the impact of temperature on latitudinal
43 distribution and diversity of phytoplankton, and to shed light on the mechanisms
44 that drive phytoplankton thermal responses in the ocean. We therefore studied the
45 thermotolerance and thermal growth response of eleven *Micromonas* strains in the
46 laboratory under controlled conditions (hereafter referred as experimental strains)
47 and we derived a mathematical model that describes the impact of temperature on
48 growth rate. With this model, we uncover the logic that lies behind the observed
49 distribution of species and their co-occurrence; we also reveal the existence of
50 thermotypes within the genus. We extrapolated the thermal response to a set of
51 46 additional strains from the Roscoff Culture Collection (hereafter referred as
52 collection strains), observed in various oceanic regions, showing that temperature
53 is the main driver of diversity and distribution in this genus. Then, we developed
54 a predictive model of niche partition to characterize *Micromonas* interspecific diver-
55 sity, which we successfully validated against the Tara Oceans dataset [27], making
56 it a plausible prediction tool. We demonstrated that *Micromonas* distribution is a
57 relevant and accurate proxy of the whole phytoplankton community distribution.
58 More than a sentinel of the ocean biogeochemistry as previously suggested by
59 Worden and colleagues [28], *Micromonas* is a probe for global warming. To explore
60 how phytoplankton communities may respond to a future, warmer ocean, we ran
61 the niche partition model under IPCC Sea Surface Temperature (SST) projections,
62 adding an evolutionary model that accounts for the potential adaptation of growth
63 to temperature changes.

64

65

RESULTS AND DISCUSSION

66 *Micromonas* strains feature distinct physiological responses to tem-
67 perature

68 To estimate the temperature tolerance and growth responses of the four described
69 *Micromonas* species, we selected three strains of *M. commoda*, *M. bravo* and *M.*
70 *pusilla* as well as two strains of *M. polaris*. We measured their exponential growth
71 rate after being grown for two months between 4°C and 35°C (41.52 ± 30.61
72 generations on average, Supplementary Table 2) depending on the strain origin.
73 To increase the accuracy in the temperature response estimation, the experimental
74 protocols followed the recommendations given in [29, 30] (see Methods). The
75 chosen strains, obtained from the Roscoff Culture Collection (RCC), were origi-
76 nally isolated from contrasted thermal niches of the Atlantic, Pacific and Artic
77 basins (Figure 1a, Supplementary Figure 3 and Supplementary Table 1). All
78 showed a typical [31, 32] asymmetric growth response to temperature, which we
79 characterized by four cardinal growth parameters: T_{min} and T_{max} , respectively
80 the minimum and maximum temperatures for growth; μ_{opt} , the maximum spe-
81 cific growth rate obtained at the optimum temperature T_{opt} (Figure 1b). Overall,
82 the *Micromonas* genus was able to grow over the thermal range tested, but with
83 diverse and specific responses for each strain, depicted by distinct cardinal pa-
84 rameters (Supplementary Table 6). Temperature stimulates enzymatic processes
85 and metabolic rates, but also accelerates cell mortality [33]. In the suboptimal
86 range ($T < T_{opt}$), enzymatic activity increases more than mortality in response
87 to increasing temperatures. At T_{opt} this balance between metabolic activity and
88 mortality is optimized and yields the highest observed net growth rate. At supra
89 optimal temperatures ($T > T_{opt}$), the denaturation of key metabolic enzymes, like
90 rubisco [34] and the thermolability of Photosystem II [35] are exacerbated, along
91 with an increase of the membrane damages [36]; as a consequence, the net growth
92 rate sharply decreases with temperature up to the maximal growth temperature
93 the strain can withstand (T_{max} at which μ is null).

94 Several patterns appeared when comparing the growth response to the annual
95 average SST (\bar{T}_S) at the site where each strain was isolated. Strains isolated in
96 locations where \bar{T}_S was above 19.7°C (RCC 299 and RCC 829) were able to grow
97 up to high temperatures ($T_{max} = 32.6 \pm 0.02$ and 37.0 ± 0.12 °C, respectively); they
98 showed a high μ_{opt} (1.1 ± 0.05 to $1.3 \pm 0.07 d^{-1}$, respectively) at an elevated opti-
99 mum T_{opt} temperature (26.3 ± 1.01 to 29.3 ± 1.2 °C, respectively). Strains isolated in
100 regions where the average SST fluctuates between 16.0 and 18.0°C presented a
101 lower optimal growth rate ($0.9 \pm 0.03 d^{-1}$) at $T_{opt} = 22.6 \pm 3.08$ °C) and maintained
102 positive growth from 4.2 ± 5.6 °C to 28.7 ± 4.63 °C. In strains isolated at sites with

103 an average temperature between 10.1 and 13.6°, μ_{opt} still reached $0.87 \pm 0.08 d^{-1}$ at
104 $T_{opt} = 23.8 \pm 0.62^\circ C$ and cells demonstrated an ability to grow over a very wide tem-
105 perature range (from $-0.7 \pm 7.46^\circ C$ to $29.4 \pm 1.55^\circ C$). Last, Arctic strains (RCC2306
106 and RCC2257) revealed both the narrowest growth temperature range ($-7.0 \pm 0^\circ$ to
107 $15.1 \pm 0^\circ C$) and lowest growth rates ($0.45 \pm 0.03 d^{-1}$) at $7.5 \pm 0^\circ C$.

108 In Summary, the four formerly described *Micromonas* species exhibited specific
109 temperature tolerance and growth optima in vitro and their according response
110 parameters were related to the thermal environment from which the strains were
111 isolated. Model parameters T_{min} , and to a lesser extent T_{max} , are difficult to
112 accurately estimate [32]. Since measurements for temperatures close to T_{min} (but
113 slightly higher) and close to T_{max} (but slightly lower) are generally rare, they must
114 be extrapolated from a mathematical model. These parameters also bracket the
115 thermal niche, i.e. the breadth of the thermal response. For instance, it appears
116 that Arctic strains showed a much narrower niche: they were more stenotherm
117 compared to the other strains.

118 The *Micromonas* genus includes six thermotypes: evidence from the
119 most recent phylogeny.

120 The phylogenetic analysis of the 57 *Micromonas* 18S DNA sequences from the
121 eleven experimental and 46 collection strains highlighted the existence of six
122 distinct phylogenetic groups (see Methods and Supplementary Figure 2). To
123 identify whether they were associated with specific thermal conditions in the
124 ocean, we analyzed available data of average SST in areas where *Micromonas* spp.
125 were sampled. We computed a non-metric dimensional scaling (NMDS) of the
126 thermal environment dataset (see Methods). The significant ordination (stress
127 = 0.004) identified six different distributions in the thermal environment, from
128 warmer, low latitudes to colder, high latitudes, that showed a good match with
129 the phylogenetic tree (Figure 2a and Supplementary Figure 3), demonstrating that
130 the thermal niche of *Micromonas* was related to its phylogenetic affiliation. *M.*
131 *polaris* and *M. pusilla* strains occupied respectively a narrow and wide thermal
132 niche while *M. bravo* and *M. commoda* each included two distinct groups. One
133 isolated from a warmer (lower latitude; warm group) and one isolated in a colder
134 (higher latitudes; cold group) environment (Figure 2a and Supplementary Figure
135 3).

136 There are few examples in the literature of latitudinal segregation within eu-
137 karyotic phytoplankton genera [37, 38]. For example, the global distribution of
138 *Ostreococcus* clades, a picoeukaryote close to *Micromonas* is related to temperature
139 but first seems to discriminate rather coastal, high-light adapted clades from
140 more oceanic, low-light adapted clades [39]. In agreement with the hypothesis of

141 Foulon *et al.* [23], our experimental and phylogenetic results showed that a niche
142 segregation within *Micromonas* did occur that is consequent to thermal, group-
143 specificities and which compels with the recently identified, four known species.
144 The present analysis further revealed the existence of two thermotypes within
145 both *M. commoda* and *M. bravo* species, making a total of six distinct *Micromonas*
146 thermotypes.

147

148 Establishing a thermal response model for *Micromonas* thermotypes

149 To obtain a better appraisal of the thermal response of strains, we looked for
150 possible correlations between cardinal growth parameters and environmental
151 features where strains had been isolated. Among the tested descriptors of the
152 SST dynamics, the average surface temperature at the isolation site (\bar{T}_S) best
153 correlated with the cardinal temperature. For T_{min} , the latitude was also included
154 in the regression (Table 1 and Supplementary Figure 6a). The optimal growth rate
155 (μ_{opt}) increased with \bar{T}_S , following the Eppley's hypothesis of a faster growth rate
156 at warmer temperatures [40]. The maximal growth temperature (T_{max}) and the
157 optimal growth temperature (T_{opt}) were also both positively correlated with \bar{T}_S ,
158 suggesting that environmental temperature featured the upper tolerance window
159 of strains. The minimal temperature of growth (T_{min}) had the lowest correlation
160 with the environmental temperature (Supplementary Figure 6b), as also reported
161 by [41] for different phytoplankton species. We found that the minimal growth
162 temperature T_{min} best correlated (negatively) with a combination of the yearly av-
163 erage temperature \bar{T}_S and latitude (Lat , Supplementary Figure 7). In the end, the
164 growth response (μ_{opt} , T_{min} , T_{opt} and T_{max}) of cultured strains can thus accurately
165 be predicted from the thermal environments (\bar{T}_S) and latitude from which they
166 were isolated, using the relations defined in Table 1. Last, statistically significant
167 correlations were also found between cardinal parameters (Supplementary Figure
168 8). In particular, the optimal temperature of growth (T_{opt}) linearly correlated with
169 the maximal temperature of growth (T_{max}) by a factor close to 1, as previously
170 highlighted for a wide range of bacterial species [42].

171

172 The relationships between cardinal growth parameters and environmental temper-
173 atures deduced from the culture experiments (Table 1) were used to extrapolate
174 the cardinal parameters of 46 additional *Micromonas* collection strains, using the
175 latitude and average annual temperature of their isolation site (Table 1 and Sup-
176 plementary Table 9). This data set confirmed a segregation of the four species into
177 six different thermotypes. To deduce a representative thermal response for each
178 thermotype, we randomly chose 100,000 values within the confidence interval

179 of the cardinal parameters of each group and ran Monte Carlo simulations of
180 the related thermal responses (see Methods). The Bernard and Rémond (BR)
181 model was then fitted to each bundle of simulated responses [32] to obtain the
182 average thermal response curve representative of each thermotype (Figure 2b and
183 Supplementary Figures 9, 10 and 11). Last, we calibrated the envelope curve,
184 inspired from [43], on the *Micromonas* genus, by fitting the BR model [32] to the
185 set of (T_{opt}, μ_{opt}) obtained for each thermotype (see Methods and Figure 2b).
186 With the narrowest thermal niche ($23.04 \pm 2.42^\circ\text{C}$), *M. polaris* was the most
187 stenotherm species. *M. commoda* cold and *M. bravo* cold showed very similar
188 responses at colder temperatures but discriminated in regard to the optimum
189 growth rate and maximum temperature. Their thermal niche of $25.42 \pm 3.75^\circ\text{C}$ and
190 $27.10 \pm 0.91^\circ\text{C}$, respectively, was representative of cold-temperate environments.
191 Contrary to the cold species, and although they both live in warmer biotopes,
192 the warm thermotype of species *M. commoda* and *M. bravo* showed very distinct
193 thermal niches ($34.00 \pm 1.19^\circ\text{C}$ and 26.02 ± 5.11 , respectively). Last, *M. pusilla*
194 was found in both cold- and warm-temperate areas and showed an intermediate
195 thermal response compared to the other *Micromonas* species, with a thermal niche
196 of $28.85 \pm 5.32^\circ\text{C}$. With the most variable response to temperature, *M. pusilla* did
197 not seem to speciate into different thermotypes; yet it clearly differentiated from
198 other groups and would be the most eurytherm.

199 Tara Oceans dataset validates the global segregation of thermotypes.
200 To validate our hypothesis that temperature is a key factor that greatly influ-
201 ences *Micromonas* biogeography over a yearly period, we retrieved the 18S V9
202 metabarcodes dataset obtained in the frame of Tara Oceans [27](Figure 3). Read
203 abundance data assigned to each of the *Micromonas* thermotypes were identified
204 across 47 stations, spanning 6 marine regions with different thermal environments:
205 Mediterranean Sea, Red Sea, Indian Ocean, South Atlantic Ocean, Southern Ocean
206 and South Pacific Ocean (Figure 3a). Using an NMDS ordination method, we
207 first compared the relative abundance of each *Micromonas* thermotype at sam-
208 pling stations (see Methods and Figure 3b) to the physicochemical environmental
209 conditions observed along the Tara Oceans circumnavigation. The presence of
210 *Micromonas* species was better explained by temperature ($R^2 = 0.48$, p -value $<$
211 0.001) than by nutrient availability, mixing, or geographical location. To a lower
212 extent, nutrients ($\text{NO}_2 + \text{NO}_3$, PO_4 and NO_2 ; $R^2 < 0.23$, p -value < 0.032), Chl *a*
213 concentration ($R^2 = 0.1710$, p -value = 0.003) and mixed layer depth (MLD; $R^2 =$
214 0.13 , p -value = 0.03) also explained significantly the *Micromonas* assemblages
215 along the transect. Temperature is thus the strongest descriptor of the change in
216 diversity between Tara Oceans stations.

217 We then compared the relative abundance of thermotypes at all stations in relation
218 to yearly SST (Figure 3c). A very clear thermal separation appeared between
219 the two *M. commoda* thermotypes, further supporting our identification of two
220 distinct thermotypes. *M. commoda* cold was most abundant in waters with tem-
221 perature below 20°C and rarely found beyond 25°C, while *M. commoda* warm
222 mostly occurred between 25°C and 30°C and was completely absent at stations
223 where temperatures were below 15°C. Species *M. bravo* was less often observed
224 than *M. commoda* and showed overlapping distributions of its two warm and cold
225 thermotypes, which we believe was due to the large thermal niche of the warm
226 thermotype spreading over that of the more restrained, cold thermotype (Figure 2).
227 A non-distinct distribution (Figure 3c) in the Tara Oceans data could also suggest
228 that the evolution of the two *M. bravo* thermotypes was more recent. Species *M.*
229 *polaris* was observed only at stations with $T < 10^\circ\text{C}$ with highest abundances near
230 0°C , validating the psychrophilic characteristics of this thermotype. Species *M.*
231 *pusilla* was only found at a few stations compared to *M. commoda* and *M. bravo*; it
232 was observed from 12°C to 30°C with a maximum abundance above 25°C . This
233 distribution may well be related to the fact that its thermal response is close to
234 the barycenter of the whole *Micromonas* thermal response (average parameters:
235 $\overline{T_{opt}} = 21.26$, $\overline{\mu_{opt}} = 0.84$ and $\overline{(T_{max} - T_{min})} = 28.34$). The reported occurrences of
236 this species at low concentrations all around the globe [23, 44] could support the
237 idea that it plays a "seed bank" role, acting as a dormancy stage of *Micromonas*
238 compared to other species [45]. Interestingly, Foulon *et al.* [23] also suggested a
239 possible niche partition over depth, along a light gradient that may explain the
240 low concentration of *M. pusilla* in the Tara Oceans dataset. In the end, temperature
241 is a sufficient parameter to describe the latitudinal segregation of *Micromonas*
242 between Tara Oceans stations. The current typology of Tara Oceans (they mainly
243 are open ocean areas), does not allow to fully assess a possible effect of nutrients
244 [46].

245 Influence of temperature on the intragenus diversity of *Micromonas* 246 assemblages

247 To further understand the thermal niche partition of *Micromonas* at the global
248 scale, we proposed a simple index to relate *Micromonas* intragenus diversity to
249 the global average SST (Figure 4 and Supplementary Figure 12). We computed
250 an interspecific *Micromonas* diversity index (Shannon derived/based) from the
251 growth response of a given thermotype i to a considered local temperature T

252 according to the equation:

$$H(T) = \sum_{i=1}^n \mathcal{D}_i \ln(\mathcal{D}_i) \text{ with } \mathcal{D}_i = \frac{\mu_i(T)}{\sum_{i=1}^n \mu_{opt,i}} \quad (1)$$

253 Where \mathcal{D}_i is the distribution index, $\mu_i(T)$ is the growth rate at the temperature
 254 T , and $\mu_{opt,i}$ is the optimal growth for the thermotype i . We compared $H(T)$ to a
 255 Shannon-like index for the *Micromonas* genus at each Tara Oceans sampling station
 256 using the proportion of each *Micromonas* thermotype OTU in the total counted
 257 *Micromonas* OTU and the local SST annual average (Figure 4a and b). Based on
 258 the calculated diversity index $H(T)$, we were able to qualitatively predict the
 259 *Micromonas* intragenus diversity estimated from the Tara Oceans V9-18S dataset
 260 (Spearman test: $\rho = 0.417$, p -value = 0.0035), thereby validating our theoretical
 261 developments. The diversity index followed a fluctuating trend through the cruise
 262 path characterized by different thermal environments (Figure 3a).

263 When running the *Micromonas* diversity model at the global scale (Figure 4c and
 264 Supplementary Figure 13), the predicted diversity was minimal at the poles (Lat
 265 $> 60^\circ\text{N}$ and $> 50^\circ\text{S}$) and at the equator (between 20°N and 20°S), especially in the
 266 Indian Ocean and the Pacific Ocean (Figure 4c). Maximum diversity levels were
 267 found from 20 to 60°N and from 20 to 40°S . We used the relationship between
 268 the phytoplankton diversity as calculated by Thomas and colleagues [3] and our
 269 *Micromonas* diversity to normalize our diversity index within Thomas's scale
 270 (see Methods). Our simulated global *Micromonas* diversity was point by point
 271 compared to the whole phytoplankton potential diversity calculated by Thomas
 272 and collaborators [3] (Figure 4d). We found a very strong relationship between the
 273 two diversity patterns ($R_{adj}^2 = 0.97$, p -value < 0.05 ; see Methods and Supplementary
 274 Figure 15). This result strongly suggests that the diversity between *Micromonas*
 275 thermotypes, at mesoscale and on a yearly basis, is representative of the whole
 276 phytoplankton community. It likely explains the overall success of the genus
 277 to colonize very contrasted biotopes [19, 23]. *Micromonas* could thus serve as a
 278 relevant marker of the biodiversity of phytoplankton communities. The term
 279 "sentinel", originally proposed by [28] to depict the role of *Micromonas* on ocean
 280 biogeochemistry is all the more relevant considering this genus reflects the pattern
 281 of the whole phytoplanktonic community and can help to better anticipate the
 282 impact of ocean warming.

283 Diversity evolution in a warmer ocean: a matter of the adaptation
284 time scale

285 To explore the impact of future temperature changes on phytoplankton diversity,
286 we investigated its evolution using SST projections over the period 2001-2100.
287 To account for the adaptation capability [4, 47], we proposed a very simple
288 adaptive model. This model assumes that the evolution time scale is related to
289 the local doubling time $\frac{\ln(2)}{\mu_i(T)}$ of each thermotype i . Adaptation is thus faster
290 for the warm thermotypes in warm environments. The adaptation dynamics
291 describes the evolution of the cardinal temperatures (T_{min} , T_{opt} and T_{max}) from
292 their present value to their value at the end of the century. The evolution rate
293 is estimated according to the characteristic number of generations Na required
294 to adapt to a different temperature, *i.e.* to shift each cardinal (i.e. represented
295 by the character "c") temperature T_c to its asymptotic value T_c^* , defined as the
296 evolutionary equilibrium given the changes of the surface temperature T at each
297 time step (Supplementary Figure 16). The evolution dynamics of each cardinal
298 parameter $T_{c,i}$ is described by a simple first order equation:

$$\frac{dT_{c,i}}{dt} = \frac{N_i(T(t))}{Na} (T_{c,i}^*(T(t)) - T_{c,i}(t)) \quad (2)$$

299 Where $N_i(T(t)) = \frac{\mu_i(T(t), T_{c,i})}{\ln(2)}$, with $\mu_i(T(t), T_{c,i}(t))$ the growth rate at the tempera-
300 ture T , calculated using the set of cardinal parameters $T_{c,i}$ for the thermotype i .

301
302 We ran this model for different Na , from fast adaptation scales ($Na < 100$ gen-
303 erations) to slow adaptation scales ($Na = 10^6$ generations) and calculated the
304 evolution of thermotypes diversity between the present period (2001 to 2010)
305 and future period (2091 to 2100, Figure 5). We considered two realistic evolution
306 hypotheses to describe the dichotomy between specialist and generalist species:
307 the Specialist-generalist hypothesis with constant thermal niche width (Figure 5a
308 and b) and the Specialist-generalist hypothesis with dynamical thermal niche [48]
309 (Figure 5c and d - see Methods). Over the 21st century, SST will globally increase
310 by 2 to 3°C over the whole ocean surface and up to 5°C around 45° N, with the
311 exception of the highest latitudes, which may see a slight decrease in their average
312 temperature (Supplementary Figure 17).

313 Similar erosion patterns were found for both specialist-generalist hypotheses that
314 showed diversity losses between 40°S to 40°N. At latitudes higher than 40°, we
315 found possible gains in biodiversity, regardless of the adaptation scenario and
316 the evolution hypothesis. At these latitudes, for most phytoplankton species, the
317 optimum temperature (T_{opt}) is higher than the average environmental temperature

318 (\bar{T}_S). With a fast adaptation scenario, thermal traits follow the thermal environ-
319 nment and T_{opt} remains above \bar{T}_S , each thermotype keeps its thermal niche and
320 diversity is not affected. In contrast, thermal traits will not change fast enough in
321 a slow adaptation scenario; \bar{T}_S gets closer to T_{opt} , and each thermotype ends up
322 with a fitness that is out of phase with the thermal environment (Supplementary
323 Figure 18). While these conditions are still favorable for growth, they typically
324 increase the diversity. Finally, for the adaptation scenario where the thermal niche
325 can increase, it gives more chance for a species to adapt faster even for a higher
326 change in the thermal environment (Supplementary Figure 19). At latitudes lower
327 than 40° , ocean warming will drive a decrease in phytoplankton diversity, with
328 a mitigation of diversity losses tightly dependent on the adaptation time scale
329 and similar for both hypotheses (Figure 5a and c). Slow adaptation scenarios
330 lead to an important diversity erosion compared to fast adaptation scenarios,
331 suggesting that the adaptation time scale is a key parameter in the mitigation of
332 diversity loss and matters far more than the strategy of adaptation itself. In areas
333 most vulnerable to diversity erosion (Supplementary Figure 20 and 21), faster
334 adaptation reduces the average diversity erosion from 4.5 species lost per latitude
335 degree (slow adaptation) to one species lost or even 2 species gained per latitude
336 (fast adaptation, Figure 5b and d). Thermal adaptation performed within 200-300
337 generations might be sufficient to mitigate the impacts of climate change on phy-
338 toplankton diversity. In contrast, an adaptation scale beyond 10^4 generations will
339 not counteract the deep impacts of climate change on phytoplankton diversity.
340 The adaptation time scale of the thermal tolerance of different phytoplankton
341 taxa has been closely related to their respective thermal environments (measured
342 with T_{opt} or the Net Primary Production) [49, 50, 51, 52]. Phytoplankton taxa
343 that ought to efficiently adapt to temperature are encountered in highly variable
344 thermal environments [49], typically found at latitudes beyond 40° , where we
345 found positive change in future diversity. These regions are also the main areas of
346 CO_2 mitigation and carbon export in the ocean [2, 53]. The deeper alteration of
347 phytoplankton diversity in the tropics might prove less critical for the efficiency
348 of the biological pump at the global scale. Future research should be addressed to
349 understand the impact of microbial diversity on carbon export [54].

350 CONCLUSION

351 This study describes niche partitioning in the marine pico-phytoplankton *Mi-*
352 *cromonas*. We showed that this genus evolved into different thermotypes that
353 discriminate according to their sensitivity to temperature. Our model predictions
354 were validated by *in situ* data from the Tara Oceans scientific expedition and
355 suggest that temperature is a robust descriptor of *Micromonas* distribution at

mesoscale and on a yearly basis. The diversity within this genus is highly correlated to the diversity pattern of the whole phytoplankton community. It is crucial to dedicate specific efforts to monitor the evolution of this sentinel genus in order to keep a real-time high fidelity picture of the phytoplankton diversity across the oceans. It is likely that *Micromonas* genus comprises even more thermotypes. More refined laboratory assessments including more thermotypes, should they exist, would enhance the representation of the global phytoplankton distribution. In particular, new experiments with smaller temperature increments and including more points at low and high temperatures would provide with a much higher resolution in the predicted capabilities and better assessment of T_{min} and T_{max} . Although decisive, the ability of phytoplankton to adapt in a warming ocean is the yet uncertain parameter. Adaptation is directly or indirectly affected by a variety of factors such as local nutrient availability, predation, virus lysis, mixing regime, etc. All of them are affected by the local physical dynamics and will also be impacted by global warming. More research is thus required to understand the adaptation mechanisms of this sentinel organism, and especially the adaptive dynamics of the different thermotypes. Such an approach will progressively refine the picture of phytoplankton evolution in a changing ocean with the possibility to more rapidly detect tipping points.

METHODS

A graphic abstract of the overall, scientific approach is provided in Supplementary Figure 1.

Growth measurements and thermal response model

Culture conditions. Eleven *Micromonas* spp. strains were selected from the RCC for the laboratory experiments. We chose strains representative of all the currently known species and according to their isolation site, to consider a range of organisms found along a latitudinal gradient (Supplementary Table 1). Cells were grown in batch cultures in ventilated polystyrene flasks (Nalgene, Rochester, NY, USA) in K-Si medium [55]. Cultures were maintained in temperature-controlled chambers (Aqualytic, Dortmund, Germany) at different temperatures (4, 7.5, 9.5, 12.5, 20, 25, 27.5, 30 and 32.5°C) for two months (see Supplementary Table 2 for the number of generations) under a 12h:12h light-dark cycle with 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ provided by fluorescent tubes (Mazda 18WJr/865).

Growth response curves. Cell concentration was determined on fresh samples using flow cytometry according to [56]. The maximum cell growth rate (μ_{max})

392 was calculated as the slope of the linear regression relating cell concentration
 393 logarithm *vs.* time observed during the exponential phase of growth. The Cardinal
 394 Temperature Model with Inflection (BR model) from [32] was used to estimate the
 395 optimal temperature of growth (T_{opt}) at which the growth rate is optimal (μ_{opt}),
 396 and the minimal and maximal temperatures of growth (T_{min} and T_{max}) at which
 397 $\mu = 0$. The growth $\mu(T)$ at temperature T is described as follows:

$$\mu(T) = \begin{cases} 0 & \text{for } T < T_{min} \\ \mu_{opt} \cdot \phi(T) & \text{for } T_{min} < T < T_{max} \\ 0 & \text{for } T > T_{max} \end{cases} \quad (3)$$

$$\text{where } \phi(T) = \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})[(T_{opt} - T_{min})(T - T_{opt}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T)]}$$

398

399 **Selection of the thermal growth response model.** Number of models exist that
 400 represent the response of phytoplankton strains to temperature; we selected the
 401 one we believe to be the most relevant for the purpose of the present study. We
 402 first short-listed the most appropriate models after the two recent reviews of [30]
 403 and [57]. Grimaud and colleagues [30] discussed the strengths and limitations
 404 of several thermal response models in regard to four criteria: the fit quality,
 405 the easiness of calibration, the biological interpretation of parameters, and the
 406 applicability to phytoplankton growth. They convincingly argued that the BR
 407 (Eq. 3, [32]) and Eppley-Norberg (Eq. 4, [58]) models presented the overall best
 408 performances. Following the analysis from [57], we also considered the Boatman
 409 model (Eq. 5, [59]) and we calibrated all three models to our growth measurements
 410 (Supplementary Figure 4 and 5).

$$\mu(T) = \left[1 - \left(\frac{T - T_{opt}}{w} \right)^2 \right] a e^{bT} \text{ where } w = \text{abs}(T_{max} - T_{min}) \quad (4)$$

$$\mu(T) = \mu_{max} \left[\sin \left(\pi \frac{T - T_{min}}{T_{max} - T_{min}} \right)^a \right]^b \quad (5)$$

411 We then computed an Akaike Information Criterion (AIC) and a Bayesian Infor-
 412 mation Criterion (BIC) for each model (Supplementary Table 5) according to the
 413 following equations:

$$AIC = 2k - 2\ln(MSE) \quad (6)$$

$$BIC = -2\ln(AIC) + k\ln(n) \quad (7)$$

414 Where k is the number of model parameters to be estimated, MSE the Mean
415 Square Error between measured and predicted growth rates and n the number of
416 data points. These two criteria provide with an estimation of the relative quality
417 of the models tested. Being an increasing function of MSE and k , the BIC is a
418 selection criterion between models. The BR model yielded the smallest criteria
419 and, in this regard, represented the best model tested to represent the growth
420 response to temperature in *Micromonas*, in agreement with the findings of [30] for
421 other phytoplankton species.

422 Phylogenetic tree reconstruction and evolutionary placements.

423 **Sequence alignment.** 18S amplicon sequences from *Micromonas* RCC strains were
424 aligned to a reference Mamiellophyceae sequence alignment. This reference align-
425 ment spans the rDNA operon and was originally used to describe the phylogenetic
426 relationships amongst Mamiellophyceae genera (Marin and Melkonian, 2010). The
427 reference alignment was trimmed to represent only the 18S rDNA region; long
428 *Micromonas* RCC 18S amplicons (> 1000 nt; $n = 35$) were added to this alignment
429 using MAFFT v7 [60]. The resulting alignment was then edited using the mask
430 from the original alignment annotation [24] and was composed of a total of 2158
431 sites.

432
433 **Phylogenetic tree reconstruction.** The edited alignment was used for maximum-
434 likelihood (ML) tree reconstructions. The best ML tree was identified from 100
435 independent tree reconstructions. All ML reconstructions were run using RAxML
436 v8 [61] with the HKY85+G+I model, which was determined as the best-fit model
437 of nucleotide substitution with jModelTest v2 [62] and by both the Akaike and
438 Bayesian information criteria. Node supports of the resulting phylogenetic tree
439 were determined using 1000 non-parametric bootstrap replicates. Bayesian in-
440 ferences were conducted using BEAST v2 [63] using the HKY85+I+G with a
441 log-normal, relaxed molecular clock and default priors. A total of 4 MCMC chains
442 of 10^6 generations were conducted, and a 25% 'burnin' value was applied on the
443 resulting tree set. The iTol web-server [64] was used to generate vector scalable
444 graphic rendering.

445
446 **Evolutionary placements.** RCC 18S amplicon sequences shorter than 1000 nt
447 ($n = 24$) were placed onto the ML phylogeny using the Evolutionary Placement
448 Algorithm (EPA) implemented in RAxML v8 [65]. Short RCC sequences were
449 aligned with MAFFT v7 against the previously generated updated reference
450 Mamiellophyceae 18S alignment (i.e., composed of reference Mamiellophyceae
451 and long RCC amplicon sequences). The aligned short sequences were then placed

452 onto the reference phylogeny using RAxML in EPA mode with the HKY85+I+G
453 model.

454

455 Thermal niche partitioning analysis.

456 **Thermal environment dataset.** Using SST from the National Oceanic and Atmo-
457 spheric Administration's (NOAA), we built a dataset gathering the environmental
458 temperatures at the isolation site of the eleven experimental and 46 *Micromonas*
459 collection strains referenced in the RCC. At each strain's isolation site, we retrieved
460 the yearly average SST (\bar{T}_S), minimum SST (T_S^-), maximal SST (T_S^+) and thermal
461 amplitude ($T_S^+ - T_S^-$) corresponding to a 10-year average (2005 to 2014).

462

463 **Thermal environment analysis.** To identify possible correlation of isolated strains
464 to temperature, a non-metric dimensional scaling (NMDS) was realized on a Eu-
465 clidean distance matrix computed on the thermal environment dataset (T_S^- , \bar{T}_S ,
466 T_S^+ , $T_S^+ - T_S^-$) using the R package *vegan* [66]. The stress value is the measure of
467 how well the NMDS configuration represents the dissimilarities and is referred as
468 the Kruskal stress [67].

469

470 **Relation between strains and environmental temperatures.** Relationships be-
471 tween environmental temperatures (T_S^- , \bar{T}_S , T_S^+ , $T_S^+ - T_S^-$), latitude of the isola-
472 tion site (Lat) and the species cardinal parameters (T_{min} , T_{opt} , T_{max} and μ_{max}) were
473 calculated for the eleven experimental strains that were grown in the laboratory.
474 We tested simple and multiple linear regression models and chose the best rela-
475 tionship according to a high $R^2_{adjusted}$ and p -value < 0.05 . Best relationships were
476 obtained with \bar{T}_S and were used to determine cardinal parameters of all other
477 46 collection strains that were not experimentally tested but referenced in the RCC.

478

479 **Thermotypes construction.** For each thermotype, we computed 100,000 growth
480 *vs.* temperature curves through a Monte Carlo procedure with the BR model
481 [32] and cardinal parameters of the i -th thermotype randomly taken from the
482 parameter distributions (assuming a gaussian repartition of the parameters in the
483 interval $[p^* - 2\sigma, p^* + 2\sigma]$ where p^* are the parameters value). In order to ensure
484 a biological coherence in the random samples of the cardinal parameters, the μ_{opt}
485 parameter is generated slightly differently. An Eppley model is used to link μ_{opt}
486 and T_{opt} [40]:

$$\mu_{opt} = a.e^{b.T_{opt}} \quad (8)$$

487 Where parameters a and b are obtained from the best fit with all the strains of the
488 thermotype (Supplementary Table 7). The values of μ_{opt} for a random strain are
489 then directly deduced from random values of T_{opt} using this model.

490 Finally, we used the BR model to get the average thermal response and its standard
491 deviation for each thermotype.

492 The optimal growth response envelope [43] for the whole *Micromonas* genus
493 was calculated with a BR curve calibrated on a data set consisting in 57 couples
494 (T_{opt}, μ_{opt}) from the eleven experimental strains and the 46 collection strains.
495 Moreover, the decreasing part of the curve was constrained with 8 couples ($T, \mu(T)$)
496 simulated from the *M. commoda* Warm thermotype model for temperatures equally
497 distributed in the (T_{opt}, T_{max}) interval for this thermotype. The increasing part of
498 the curve was also constrained with eleven couples ($T, \mu(T)$) simulated from the
499 *M. polaris* model for temperatures equally distributed in the (T_{min}, T_{opt}) interval
500 for this species.

501 Tara Oceans

502 **Tara Oceans V9 dataset analysis.** Molecular and contextual data from the Tara
503 Oceans project were retrieved from PANGAEA [68]. The Tara Oceans V9-18S
504 dataset [27] is available both at the barcode level (non-redundant sequences) and
505 clustered at the Swarm/operational taxonomic unit level [69]. *Micromonas*-like
506 V9-18S barcode sequences were retrieved based on the original taxonomic classifi-
507 cation from the Tara Oceans consortium, which was conducted with the Protist
508 Ribosomal Reference database [70] for the protist barcode subset. The resulting
509 1084 non-redundant barcodes classified as *Micromonas*-like, and which represented
510 a total of 95755 occurrences across the V9-18S Tara Oceans sampling (334 sam-
511 ples from 47 stations), were then re-classified using a phylogenetic placement
512 procedure. The non-redundant *Micromonas*-like V9-18S barcodes were aligned
513 against a reference Mamiellophyceae alignment using the same methodology
514 than for the short 18S amplicon sequences from the *Micromonas* RCC strains,
515 as aforementioned. The V9-18S barcode sequences were then placed onto the
516 Mamiellophyceae and RCC reference tree using RAxML EPA with the HKY85+I+G
517 model. Based on the placement of the Tara Oceans barcode onto the *Micromonas*
518 reference subtree, the corresponding taxonomic information (thermotype level)
519 was assigned to the environmental barcode.

520
521 **Thermotypes inside the Tara Oceans V9 dataset.** To explore the impact of tem-
522 perature on species occurrence, we computed an NMDS on a Bray-Curtis distance
523 matrix calculated from a community matrix of *Micromonas* species abundance per
524 station (expressed in percentage of barcodes) with the R package "vegan" [66].

525 Results display a cloud of sampling stations from the different oceanic basins, dis-
 526 criminating surface and deep chlorophyll maximum (DCM); the closer proximity
 527 of stations, in terms of Bray-Curtis distances, expresses their similarities in their
 528 18S diversity. We then fitted environmental variables (nutrients, temperature and
 529 mixed layer depth) and total chlorophyll *a* abundance on the ordination space
 530 with the vegan function *envfit* in vegan package [66] with *p*-value based on 999
 531 permutations was used to assess the significance of the fit.

532 The *Micromonas* distribution for each thermotype was computed against yearly
 533 SST (from NOAA) for each Tara Oceans station. We then computed Loess regres-
 534 sions with polynomial fitting to illustrate the temperature patterns with the R
 535 package "ggplot2" [71].

536 Global temperature response and diversity index

537 **Global SST dataset.** We used global SST data from the Copernicus Marine Envi-
 538 ronment Monitoring Service (product: GLOBAL_REP_PHYS_001_013) to calculate
 539 monthly averages SST in the period 1993 - 2012 at the global scale.

540
 541 **Species distribution as a function of temperature.** Cardinal parameters (T_{min} ,
 542 T_{opt} , T_{max}) and optimum growth rate μ_{opt} for each thermotype i were used to
 543 calculate the growth rate $\mu_i(T)$ for each temperature T using the BR model [32].
 544 Then, normalized distribution $\mathcal{D}_i(T)$ of each thermotype was calculated following
 545 the equation: $\mathcal{D}_i(T) = \frac{\mu_i(T)}{\sum_{i=1}^n \mu_{opt,i}}$ for each temperature T of the global ocean surface.
 546 Remark that this normalisation removes the effect of other factors which also
 547 influence net growth at the same location (nutrients, light, predations, etc.).

548
 549 **Diversity index.** To get a diversity index, we computed 10,000 thermal distribu-
 550 tion via a Monte Carlo procedure for each species (Supplementary Figure 13).
 551 We then computed an averaged and standard deviation of a Shannon-like based
 552 interspecific diversity index within the *Micromonas* genus according to Eq. 1
 553 (Supplementary Figure 14) and compared it with a Shannon diversity index based
 554 on Tara Oceans V9 dataset thermotypes relative abundance:

$$H_{TARA}(s) = \sum_{i=1}^n E(s,i) \ln(E(s,i)) \quad (9)$$

555 Where $E(s,i)$ is the number of barcodes for the *Micromonas* thermotype i at the
 556 station s . The Tara Oceans dataset was used along the transect from station 4 to
 557 125 [27]. The spatial distance between stations was calculated as a distance as the
 558 crow flies. In addition, we compare the Shannon-like base interspecific diversity

559 index (Eq. 1) calculated for *Micromonas* (H_M) to the diversity index calculated
 560 by Thomas and colleagues for the phytoplankton (H_P) with a linear regression
 561 model ($R_{adj}^2 = 0.95$ and p -value < 0.5):

$$H_P = 83.21H_M + 65.05 \quad (10)$$

562 Then, we used Eq. 10 to quantify the diversity in the same index as the Thomas *et*
 563 *al.* study [3] (Supplementary Figure 15).

564 Cardinal parameters adaptation model

565 **Cardinal Parameters Evolution.** We studied the evolution of diversity in a warmer
 566 ocean with a dynamical model of the thermal growth response over the period
 567 2001 to 2100. Projections of future, global temperature regimes were obtained
 568 from the NOAA GFDL CM2.1 [72, 73] driven with the SRES A2 emissions scenario
 569 [74]. This dataset spans from 2001 to 2100 and was also used by Thomas and
 570 colleagues [3].

571 First, we computed the evolution of cardinal parameters $T_{c,i}$ (T_{min} , T_{opt} and T_{max})
 572 for each thermotype i depending on the temperature $T(t, l, L)$ with t the year, l
 573 the latitude and L the longitude. The evolution of cardinal parameters follows Eq.
 574 2, which is parameterized by the number of generations Na required to adapt to
 575 a different temperature (Supplementary Figure 16):

$$\frac{dT_{opt,i}}{dt} = \frac{N_i(T(t))}{Na} (T_{opt,i}^*(T(t)) - T_{opt,i}(t)) \quad (11)$$

576

$$\frac{dT_{max,i}}{dt} = \frac{N_i(T(t))}{Na} (T_{max,i}^*(T(t)) - T_{max,i}(t)) \quad (12)$$

577 Where $T_{opt,i}^*$ and $T_{max,i}^*$ are computed from the derivative of the relationships in
 578 Table 1 depending on the local temperature $T(t, l, L)$:

$$\frac{dT_{opt,i}^*}{dt} = 0.84 \frac{dT(t, l, L)}{dt} \quad (13)$$

579

$$\frac{dT_{max,i}^*}{dt} = 0.77 \frac{dT(t, l, L)}{dt} \quad (14)$$

580 The evolutive minimal temperature of growth was computed contingent to the

581 evolution hypothesis:

$$T_{min,i}^* = \begin{cases} T_{min,i}^{ini} + T_{max,i}^* - T_{max,i}^{ini} & \text{Constant thermal niche} \\ \frac{dT_{min,i}}{dt} = \frac{N_i(T(t))}{Na} (T_{min,i}^*(T(t)) - T_{min,i}(t)) & \text{Dynamical model (Eq. 2)} \end{cases} \quad (15)$$

582 Where $T_{min,i}^{ini}$ and $T_{max,i}^{ini}$ are the initial value of $T_{min,i}$ and $T_{max,i}$ respectively at time
 583 $t = 2001$ and $T_{min,i}^*$ is computed from the derivative of the relationships in Table 1
 584 depending on the local temperature $T(t, l, L)$:

$$\frac{dT_{min,i}^*}{dt} = -0.92 \frac{dT(t, l, L)}{dt} \quad (16)$$

585 We constrained $T_{min,i}^*$ and $T_{max,i}^*$ by the envelope curve [43] of the *Micromonas*
 586 genus (Figure 2b) that represents its evolution boundaries.

587 Second, we calculated $\mu_{opt,i}$ at $T_{opt,i}$ with the BR model calibrated with the cardinal
 588 parameters of the envelope curve.

589 Third, we calculated the related growth rate $\mu_i(T)$ of each thermotype i depending
 590 on its cardinal parameters $T_{c,i}$ at temperature $T(t, l, L)$ following the BR model
 591 [32].

592 Third, we calculated the diversity for the present (2001 to 2010 - H_{now}) and future
 593 (2091 to 2100 - H_{future}) periods following the Eq. 1 averaged on 10 years and
 594 expressed as the diversity index used by Thomas and colleagues [3] with the Eq.
 595 10.

596
 597 **Diversity erosion.** We performed this cardinal parameter evolution framework
 598 for different values of Na , from fast ($Na < 100$ generations) as highlighted by
 599 [50, 51] to slow ($Na = 10^9$) adaptation kinetics. This slow time scale corresponds
 600 to two to six months in the lab, which means a time scale in the range of years
 601 in the natural environment (assuming $\mu = 0.2 \text{ day}^{-1}$ as a typical growth rate in
 602 the sea). For long-term evolution, we refer to a time scale slower than climate
 603 change. We call slow evolution an evolution with a typical adaptation kinetics
 604 with a millennium, which means $Na = 10^6$ generations for an average growth
 605 rate of 0.2 day^{-1} . We then calculated a diversity erosion index representing the
 606 loss of diversity along the latitude gradient with the equation:

$$H_{erosion}(l) = \frac{h_L}{L_{max}} \sum_{L=0}^{L_{max}} (H_{now}(l, L) - H_{future}(l, L)) \quad (17)$$

607 With L the longitude and l the latitude, L_{max} the maximal longitude of the dataset
 608 ($n = 359.7$) and h the longitude resolution ($h_L = 0.1$).

609 The averaged latitudinal erosion ($\overline{H_{erosion}}$) per latitude was calculated as follows:

$$\overline{H_{erosion}} = \frac{h_l}{n} \sum_{l=l_{min}}^{l_{max}} (H_{erosion}(l)) \quad (18)$$

610 With l the latitude, l_{min} and l_{max} the minimum and maximum latitude of the
611 dataset ($l_{min} = -82$ and $l_{max} = 90$), h_l the latitude resolution ($h_l = 0.1$) and n the
612 $H_{erosion}$ vector's length. A negative erosion signifies a diversity gain.

613 The tipping point (p) of the $\overline{H_{erosion}}$ vs. Na curve was calculated as the inflection
614 point following the equation:

$$p = \max \left(\frac{d\overline{H_{erosion}}}{dNa} \right) \quad (19)$$

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CONFLIT OF INTEREST STATEMENT

835 Authors declare no conflict of interest for this study.

836

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844

AUTHOR CONTRIBUTIONS

845 D.D., A-C.B., O.B., N.S., A.S. and S.R. designed the study. D.D., A-C.B., N.S.,
846 P.G., F.R-J. carried out the experiments. D.D. and O.B. carried out the modeling
847 and statistical analyses. D.D. provided the display items. A.M. carried out the
848 phylogenetic and Tara Ocean V9 dataset analysis. C.S. and D.M. helped technically.
849 D.D., O.B. and S.R. wrote the manuscript with contributions from N.S., C.S. and
850 A-C.B.

851

FIGURE AND TABLE LEGENDS

Figure 1: *Micromonas* growth response to temperature. (a) Location of isolation sites of the eleven *Micromonas* experimental strains used in this study, plotted against yearly average SST for the year 2014 (from NOAA). (b) Growth rate vs. temperature curves for strains isolated in environments with different annual average temperature (\bar{T}_S), fitted by the BR model [32]. Error bars are standard deviations ($n \geq 3$).

Table 1: *Linear relationship between cardinal parameters and environmental parameters (average temperature at the surface of isolation site, \bar{T}_S , and the latitude, Lat) for the eleven *Micromonas* experimental strains tested in this study.*

Figure 2: Original thermal environments and growth response to temperature for *Micromonas* species. (a) Two-dimensional ordination space derived from a Non-Metric MultiDimensional Scaling (NMDS) procedure displaying the thermal dissimilarities site (T_S^- , \bar{T}_S , T_S^+ and $T_S^+ - T_S^-$) between the original isolation sites of the eleven experimental and 46 *Micromonas* collection strains. The stress value (goodness-of-fit of the NMDS) is inferior to 0.05, indicating high dimensional relationships among samples. (b) Average growth response to temperature for each phylogenetic group computed from 100,000 possible response curves simulated within the ranges observed in each phylogenetic group. The black line represents the overall, optimal growth response envelope [43] of *Micromonas* computed as μ_{opt} vs. T_{opt} , where μ_{opt} and T_{opt} are given by the average response of each thermotype. The grey shaded area is the standard deviation around μ_{opt} .

Figure 3: *Micromonas* thermotypes relative abundance patterns as estimated from the 18S rRNA V9 region during the Tara Oceans cruise. (a) Map of the Tara Oceans transect (dashed black line) showing station for which 18S rRNA V9 region data were available from Vargas et al. (2015) [27]: Mediterranean Sea (Med S), Red Sea (Red S), Indian Ocean (Ind O), South Pacific Ocean (S Pac O), Southern Ocean (S O) and South Atlantic Ocean (S Atl O). (b) Two-dimensional ordination space derived from an NMDS analysis displaying Bray-Curtis distance between the *Micromonas* species assemblages of the Tara Oceans stations, fitted by significant environmental variable (p -value < 0.05). The stress value (goodness-of-fit of the NMDS) is 0.15, indicating fair dimensional relationships among samples. (c) Relative abundance of the 6 thermotypes per station, plotted according to yearly SST at station coordinates: data (circles) and polynomial regression (solid line) fitted with the 95% confidence interval (shaded area). Number of observations for the 6 thermotypes are represented in histograms, plotted according to yearly SST at station coordinates.

Figure 4: *Estimated and predicted interspecific diversity within the Micromonas genus in the global ocean. (a) Estimated and predicted interspecific diversity within the Micromonas genus along the Tara Oceans transect as estimated from the Micromonas OTUs read abundances (blue circles) and as predicted from our diversity model (red circles), fitted by a polynomial regression with a 95% confidence interval. (b) Thermotypes proportions (%) from Tara Oceans dataset for different oceanic regions: Mediterranean Sea (Med S), Red Sea (Red S), Indian Ocean (Ind O), South Pacific Ocean (S Pac O), Southern Ocean (S O) and South Atlantic Ocean (S Atl O). (c) Predicted Shannon diversity index (H) calculated with the equation 1 using annual averages SST (Copernicus Marine Environment Monitoring Service, 1993 to 2012 satellite data). (d) Comparison of the latitudinal average diversity for all phytoplankton (from Thomas et al. 2012. black line) with that estimated by our Micromonas model. Shaded area represents the standard deviation from the mean along latitudes.*

Figure 5: *Micromonas diversity changes in a warming ocean for two evolution hypotheses: (a-b) Specialist-generalist with constant thermal niche and (c-d) Specialist-generalist with dynamical thermal niche. (a-b) Latitudinal averaged diversity erosion calculated as the difference between diversity in present period (2001 to 2010) and future (2091 to 2100). Black line represents the diversity erosion from Thomas et al. 2012, red and blue line are the diversity erosion for the fast adaptation scenario ($N_a = 100$) and slow adaptation scenario ($N_a = 10^6$) respectively. Filled area represent the standard deviation to the mean along latitude. (c-d) Averaged diversity erosion per latitude calculated for different adaptation kinetic (from $N_a = 1$ to $N_a = 10^6$ generations): model results (black circles) and polynomial regression (blue line) fitted. The Tipping point is calculated as the inflexion point for the derivative of blue curve. The 20% loss point is calculated as 20% evolution from the lowest erosion scenario ($N_a = 1$).*

Picoeukaryotes of the *Micromonas* genus: sentinels of a warming ocean

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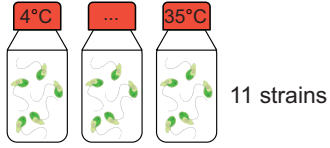
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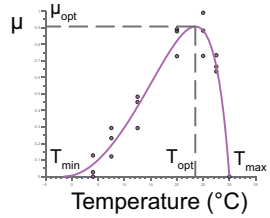
May 15, 2018

Micromonas thermal responses

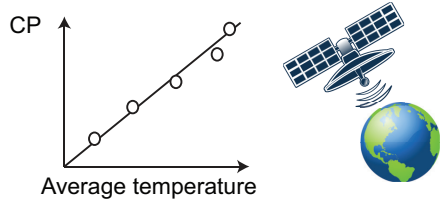
1) Thermal response experiments in laboratory



2) BR model fits to obtain cardinal parameters (CP)



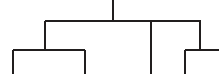
3) Relationships between cardinal parameters (CP) and thermal environment data from NASA



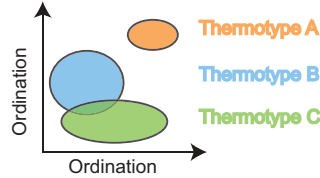
4) Extension of the 11 experimental strains to 46 additional collection strains to create a dataset of temperature response with 57 *Micromonas* strains.

Thermotype definition

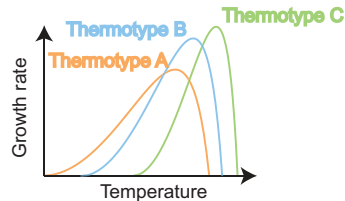
5) Phylogeny from 18S sequences for the RCC *Micromonas* strains



Thermotypes definition thanks to the phylogeny, the thermal response and the thermal environment for each strain with statistical ordination methods



6) Exploration of the Tara Oceans data set to validate our theoretical results

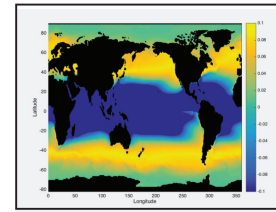


Biogeography

7) Theoretical calculus of the thermotype distribution at the global scale with SST data-set



8) Summary of the distribution with a Shannon like diversity index related to the thermal response of each thermotype



9) Exploration of the Tara Oceans data set to validate our theoretical results



10) Comparison with Phytoplankton diversity from Thomas *et al.* 2012



11) Evolution of phytoplankton thermal niche with an adaptive model using future SST projection from IPCC and a simple thermal traits dynamical model

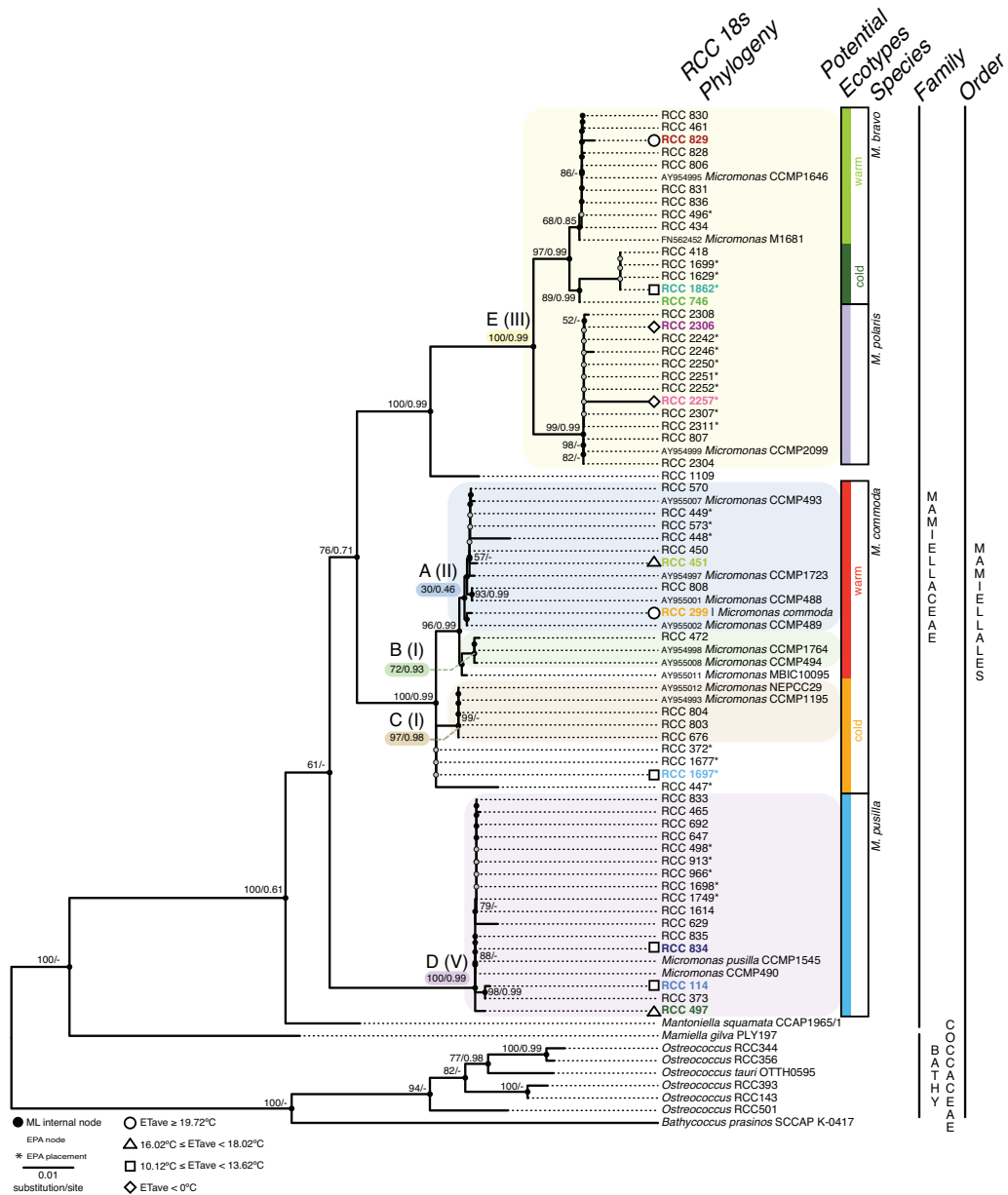
Choice of the light intensity during the experiments

The experiments were conducted at $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ to find an optimal trade-off between non-photolimiting and non-photoinhibiting conditions. As supported by the work of [1], temperature growth response of phytoplankton is weakly coupled with light intensity for moderate light, whereas it could become more dependent to light at higher light intensities for which photoinhibition occurs. [2] showed that marked light-limitation can reduce the optimal growth temperature of phytoplankton by about 5°C . [3] studied the light growth response of *Micromonas commoda* and observed photoinhibition for light intensities higher than $300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

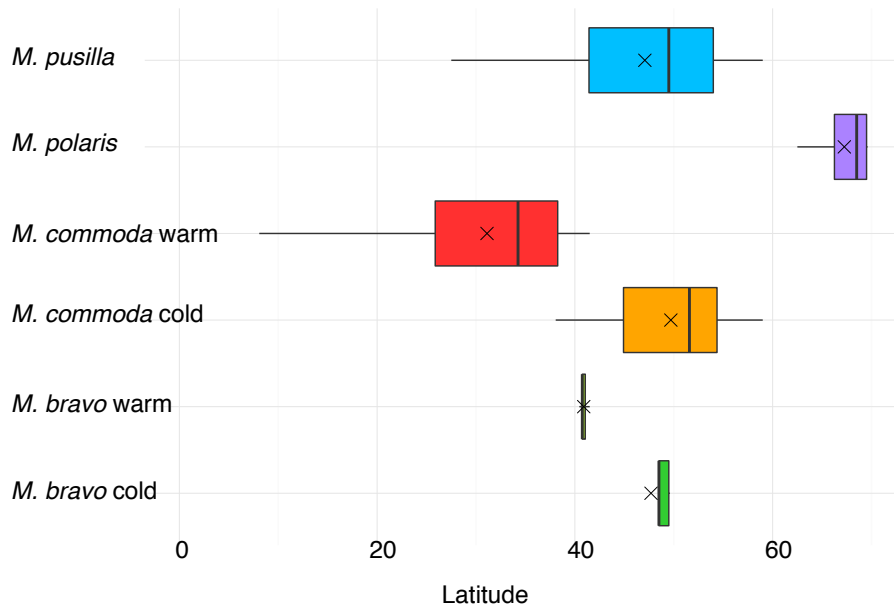
In order to develop a model that accounts for the response to temperature, it was critical to experiment on the potential response, i.e. to assess the maximum growth capacity of strains at each temperature, not to introduce any bias (such as photoinhibition) in the experiments that would have led to an inaccurate estimation of the sole impact of temperature. The intensity of $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ was therefore a reasonable trade-off. The BR model being tailored to account for light limitation on growth as well, it would then be possible to describe the coupled limitation of light and temperature, should it appear necessary. However, in the present study, the model proved to accurately compare to in situ data sets with the sole response to temperature, which indicated that additional model complexity through the inclusion of a light response was not necessary

Supplementary Table 1: Information regarding the *Micromonas* strains used in the study. The thermal environment at the isolation sites is expressed in °C: yearly averaged temperature (\bar{T}_S), minimal temperature (T_S^-), and maximal temperature (T_S^+). The latitude of each isolation site (Lat) is expressed in degree and the growth temperature of cultures (T_{RCC}) is in °C.

RCC #	Species	Thermotype	T_{RCC} (°C)	\bar{T}_S (°C)	T_S^- (°C)	T_S^+ (°C)	Lat (°)
114	<i>pusilla</i>		20	11.48	3.85	20.63	41.5
299	<i>commoda</i>	Warm	20	24.89	22.7	27.23	22
451	<i>commoda</i>	Warm	20	17.67	10.99	25.34	38.5
497	<i>pusilla</i>		20	18.02	13.07	24.2	41.5
746	<i>bravo</i>	Cold	15	16.02	13.23	19.31	42.5
829	<i>bravo</i>	Warm	20	19.72	14.00	26.73	40.75
834	<i>pusilla</i>		20	12.77	9.08	16.73	50.5
1697	<i>commoda</i>	Cold	15	10.12	5.76	15.90	59
1862	<i>bravo</i>	Cold	15	13.62	9.91	17.58	48.5
2257	<i>polaris</i>		4	-0.38	-1.79	3.11	71
2306	<i>polaris</i>		4	-0.33	-1.79	3.21	71



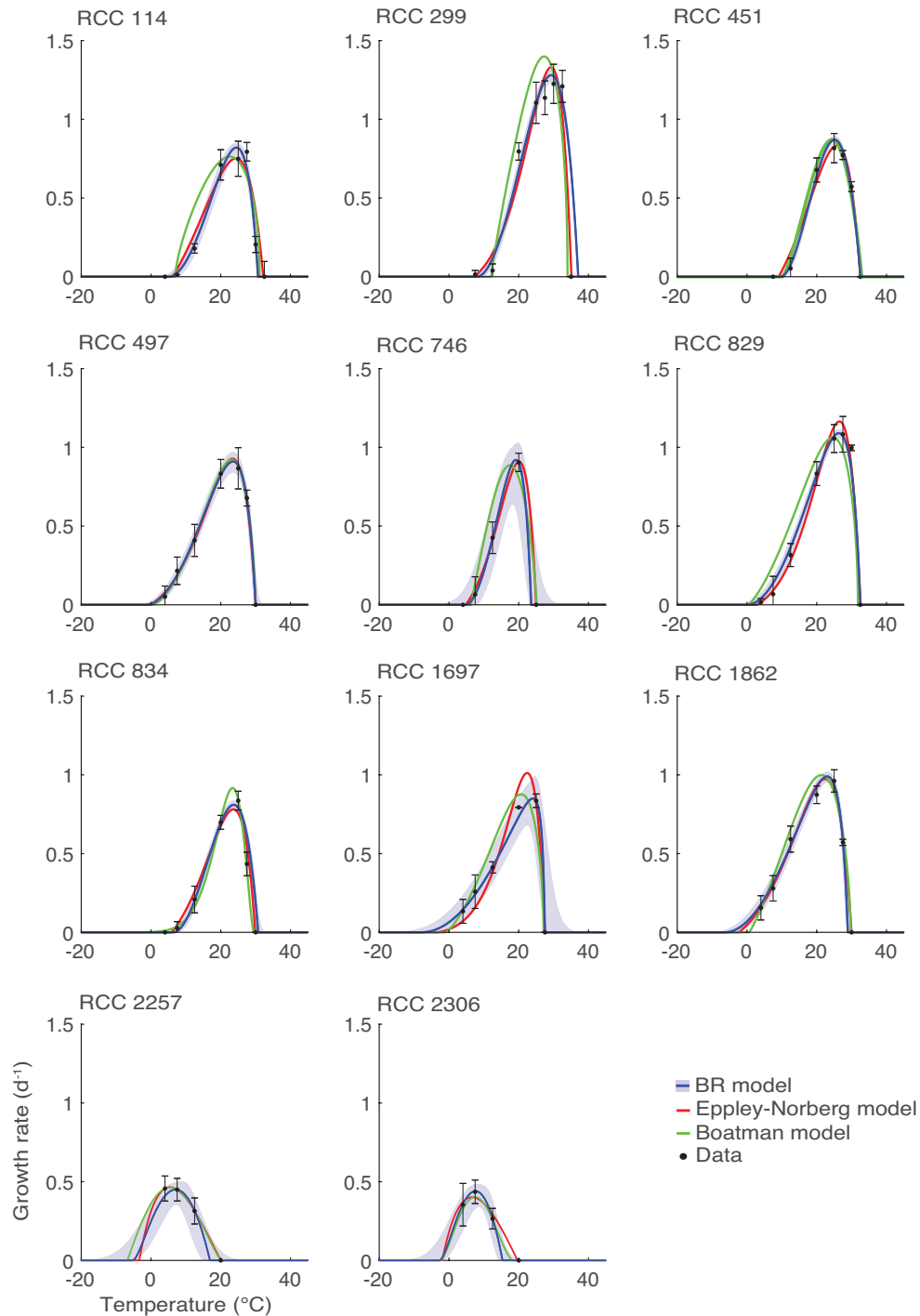
Supplementary Figure 2: Phylogenetic analysis on 82 18S sequences of RCC strains based on the alignment of [4].



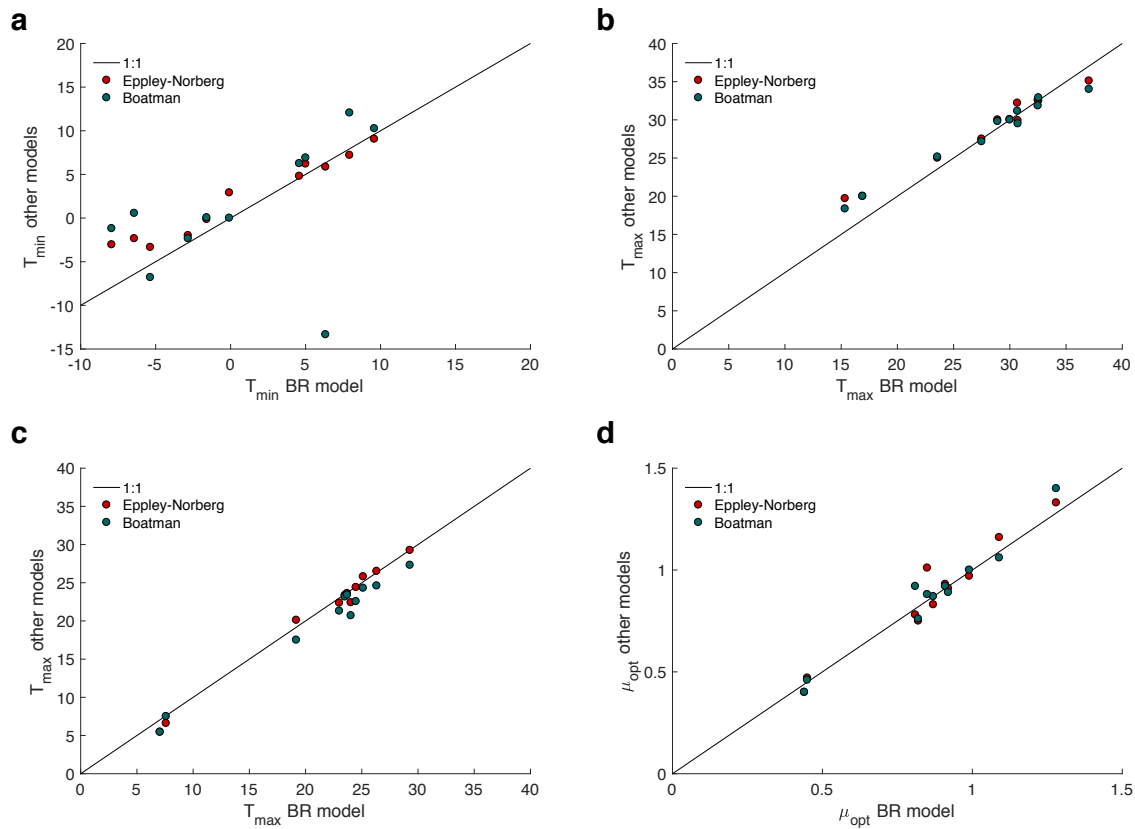
Supplementary Figure 3: Boxplot of the latitude at which the six phylogenetic groups of *Micromonas* were isolated

Supplementary Table 2: Number of generations during the two-month acclimation calculated with cardinal parameters in Table 6. Symbol “–” indicates a null growth rate.

RCC #	4°C	7.5°C	9.5°C	12.5°C	20°C	25°C	27.5°C	30°C	32.5°C	35°C
114	–	2.21	6.97	18.37	58.31	71.89	60.06	19.31	–	–
299	–	–	1.08	8.66	53.85	93.38	108.39	111.77	88.39	–
451	–	–	0.03	7.85	57.41	76.56	69.92	46.59	1.84	–
497	6.49	16.62	24.18	37.41	72.39	77.87	58.93	–	–	–
746	–	5.72	15.65	37.37	79.35	–	–	–	–	–
829	1.61	8.56	14.85	26.13	68.02	92.23	94.28	75.91	0.54	–
834	–	1.95	6.47	17.74	60.92	73.60	38.08	–	–	–
1697	12.77	21.22	26.94	36.65	64.63	73.27	–	–	–	–
1862	15.75	27.48	35.38	48.47	81.22	82.49	50.99	–	–	–
2257	35.44	41.36	39.02	24.78	–	–	–	–	–	–
2306	32.42	37.84	35.70	22.67	–	–	–	–	–	–



Supplementary Figure 4: Growth thermal response model fits for the 11 experimental strains. BR model (blue, solid line) with its 95% confidence interval (blue, shaded area), Eppley-Norberg model (red, solid line; [5]), Boatman model (green, solid line, [6]) and average experimental data (black circles) with their standard deviation (n at least = 3).



Supplementary Figure 5: Comparison of cardinal parameters from the three thermal response models tested. (a) T_{min} . (b) T_{max} . (c) T_{opt} . (d) μ_{opt}

Supplementary Table 3: Comparison of three models of growth thermal response. AIC is the Akaike Information Criterion calculated as follows: $AIC = 2k - 2\ln(MSE)$, with k , the number of parameters to be estimated and MSE , the Mean Square Error calculated with the best fits represented in Supplementary Figure 4. BIC is the Bayesian Information Criterion calculated as follows: $BIC = -2\ln(AIC) + k\ln(n)$, with n , the number of experimental data used for the estimation of the parameters. Minimum values of AIC and BIC represent the best model according to the number of estimated parameters and the quality of the fit.

Model	Number of parameters	AIC	BIC
BR	4	89.22	178.58
Eppley-Norberg	4	89.35	178.57
Boatman	5	110.51	225.04

Supplementary Table 4: *Parameters of the Eppley-Norberg model [5] for the eleven experimental strains. Parameters were estimated by minimizing the Mean Squared Error (MSE) between model fit and data with the "fminsearch" Matlab function implementing the Nelder-Mead simplex algorithm as described in [7]. The stars in the table indicate that the parameter is explicitly written in the model. The optimal growth rate μ_{opt} is not explicit in the model and is then deduced from the thermal response.*

Strains	T_{min}^*	T_{opt}^*	T_{max}^*	μ_{opt}
114	6.20	24.40	32.20	0.75
299	7.20	29.25	35.10	1.33
451	9.05	25.80	32.50	0.83
497	-0.15	23.35	30.05	0.93
746	4.8	20.10	25.00	0.91
829	2.9	26.50	32.60	1.16
834	5.85	23.60	29.90	0.78
1697	-3.05	22.40	27.50	1.01
1862	-2.35	22.35	30.00	0.97
2257	-3.35	5.45	20.00	0.47
2306	-2.00	6.6	19.7	0.40

Supplementary Table 5: *Parameters of the Boatman model [6] for the eleven experimental strains. Parameters were estimated by minimizing the Mean Squared Error (MSE) between model fit and data with the "fminsearch" Matlab function implementing the Nelder-Mead simplex algorithm as described in [7]. The stars in the table indicate that the parameter is explicitly written in the model. The optimal temperature of growth T_{opt} is not explicit in the model and is then deduced from the thermal response.*

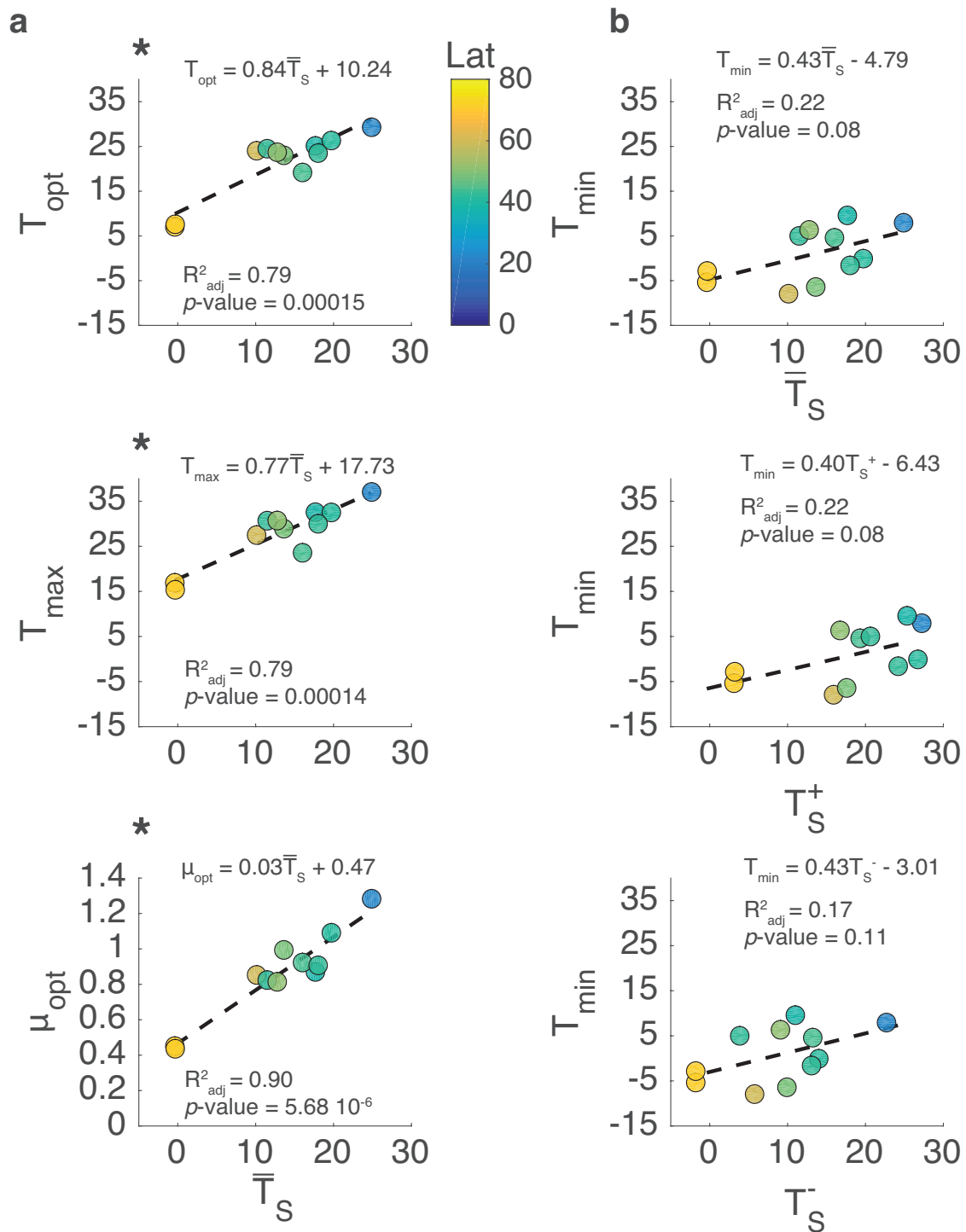
Strains	T_{min}^*	T_{opt}	T_{max}^*	μ_{opt}^*
114	6.90	22.55	31.15	0.76
299	12.05	27.30	34.00	1.40
451	10.25	24.30	32.90	0.87
497	0.05	23.15	30.00	0.92
746	6.25	17.50	25.15	0.89
829	0.00	24.60	31.85	1.06
834	-13.35	23.40	29.50	0.92
1697	-1.20	20.70	27.15	0.88
1862	0.55	21.30	29.80	1.00
2257	-6.80	5.45	20.00	0.46
2306	-2.35	7.50	18.35	0.40

Supplementary Table 6: Cardinal parameters estimated with the BR model for the eleven strains tested experimentally. Parameters are expressed in °C: minimal temperature of growth (T_{min}), optimal temperature of growth (T_{opt}) and maximal temperature of growth (T_{max}). The optimal growth rate (μ_{opt}) is expressed in day^{-1} . The under and over lines on cardinal parameters represent the lower and upper 95% confidence intervals for each parameter respectively.

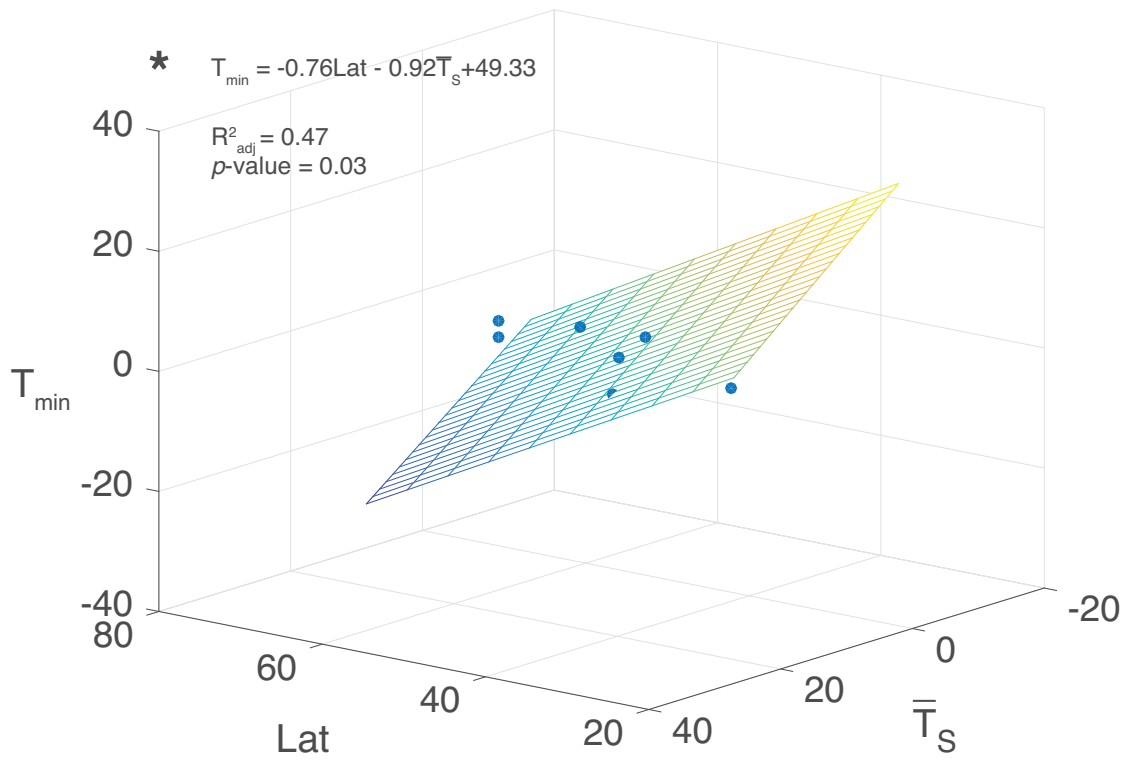
RCC #	$\underline{T_{min}}$	T_{min}	$\overline{T_{min}}$	$\underline{T_{opt}}$	T_{opt}	$\overline{T_{opt}}$	$\underline{T_{max}}$	T_{max}	$\overline{T_{max}}$	$\underline{\mu_{opt}}$	μ_{opt}	$\overline{\mu_{opt}}$
114	1.01	5.01	8.63	22.68	24.49	26.34	30.00	30.68	31.27	0.76	0.82	0.89
299	5.34	7.94	10.32	28.15	29.29	30.56	36.91	37.05	37.14	1.21	1.28	1.35
451	7.53	9.59	11.49	24.49	25.13	25.83	32.44	32.56	32.65	0.82	0.87	0.92
457	-4.36	-1.59	2.54	22.04	23.51	24.42	29.31	30.00	31.94	0.77	0.91	1.00
746	-2.76	4.59	11.16	14.17	19.18	22.18	16.44	23.57	26.26	0.59	0.92	1.06
829	-3.61	-0.08	3.47	25.32	26.33	27.34	32.49	32.51	32.53	1.04	1.09	1.14
834	3.32	6.34	8.86	22.73	23.71	24.69	29.32	30.72	31.90	0.76	0.81	0.87
1697	-16.04	-7.93	2.44	20.38	24.04	25.64	25.50	27.50	35.95	0.73	0.85	1.14
1862	-11.64	-6.42	-1.71	21.87	23.01	24.35	27.59	28.92	29.81	0.94	0.99	1.06
2257	-14.12	-5.35	8.76	4.35	7.03	11.13	8.04	16.91	22.50	0.35	0.45	0.54
2306	-9.74	-2.83	7.58	4.68	7.60	12.03	11.00	15.35	18.37	0.31	0.44	0.53

Supplementary Table 7: Parameters of of the Eppley model [8] for the 6 thermotypes. The Eppley model equation is: $\mu_{opt} = a \cdot e^{b \cdot T_{opt}}$. The parameters a and b are obtained from the best fit between μ_{opt} and T_{opt} considering all strains within each thermotype.

Thermotype	a	b
<i>M.commoda</i> Cold	0.39	0.04
<i>M.commoda</i> Warm	0.2	0.06
<i>M.polaris</i>	0.34	0.03
<i>M.bravo</i> Cold	0.28	0.05
<i>M.bravo</i> Warm	0.88	0.007
<i>M.pusilla</i>	0.39	0.04



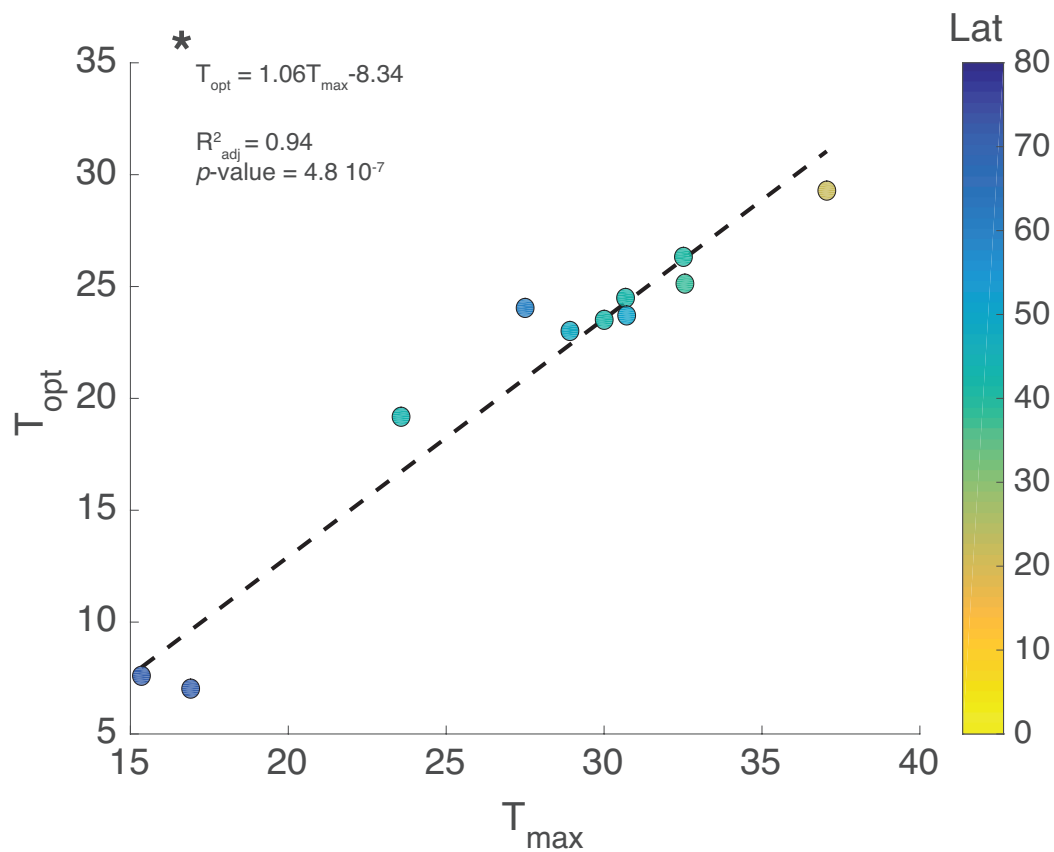
Supplementary Figure 6: Linear relationships between cardinal parameters and environmental parameters for the eleven strains tested experimentally. a) Relationships between T_{opt} , T_{max} and μ_{opt} vs. the average surface temperature at the isolation site \bar{T}_S . b) Relationships between T_{min} vs. averaged surface temperature at the isolation site \bar{T}_S , maximal surface temperature at the isolation site T_S^+ and minimal surface temperature at the isolation site T_S^- . Latitude at the isolation site is expressed with the color-bar. The star on top of the vertical axis represents a statistical significant relationship ($p\text{-value} < 0.05$).



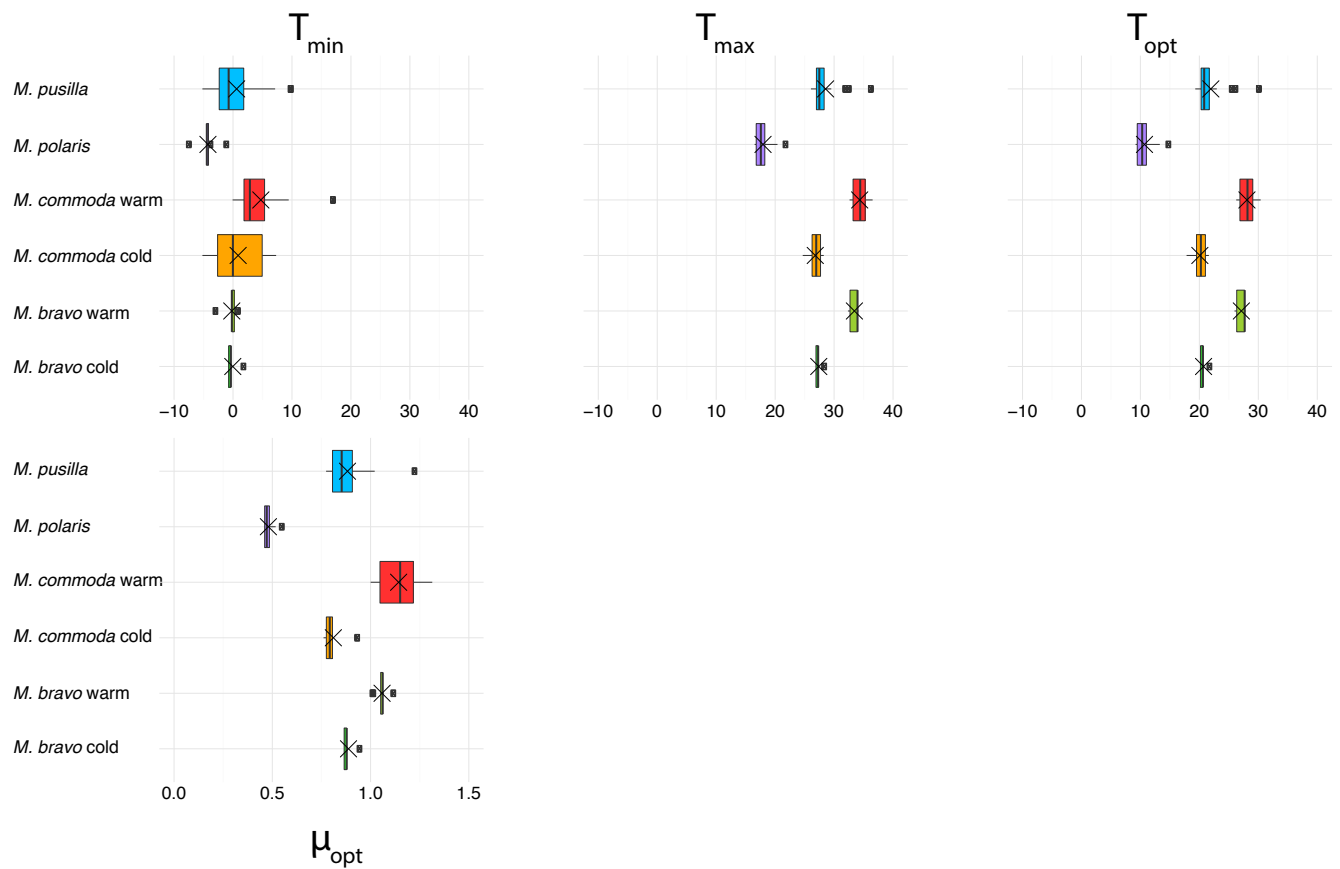
Supplementary Figure 7: Linear relationships between T_{\min} vs. the latitude at the isolation site Lat and the average surface temperature at the isolation site \bar{T}_S for the eleven strains tested experimentally. The star on top of the vertical axis represents a statistical significant relationship (p -value < 0.05).

Supplementary Table 8: Cardinal parameters (in °C), optimal growth rate (in day⁻¹) and thermal niche width (in °C) of the six thermotypes with their associated standard deviation.

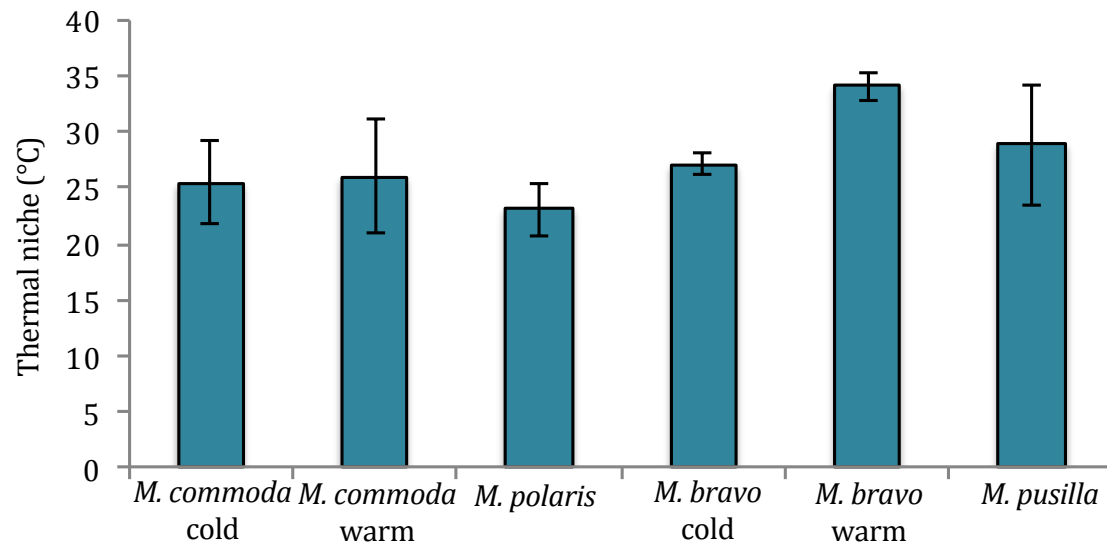
Thermotypes	T_{min}	T_{opt}	T_{max}	μ_{opt}	Thermal niche
<i>M. commoda</i> cold	0.15 ± 5.06	20.11 ± 1.38	26.84 ± 1.30	0.78 ± 0.04	26.69
<i>M. commoda</i> warm	4.53 ± 5.15	27.96 ± 1.42	34.39 ± 1.34	1.10 ± 0.10	29.86
<i>M. polaris</i>	-4.53 ± 1.38	10.55 ± 1.76	18.21 ± 1.66	0.45 ± 0.03	22.74
<i>M. bravo</i> cold	-0.11 ± 1.15	20.67 ± 0.71	27.40 ± 0.67	0.88 ± 0.03	27.51
<i>M. bravo</i> warm	-0.24 ± 1.13	27.03 ± 0.78	33.41 ± 0.74	1.05 ± 0.005	33.65
<i>M. pusilla</i>	-0.11 ± 4.84	21.22 ± 3.01	29.46 ± 2.84	0.78 ± 0.11	29.57



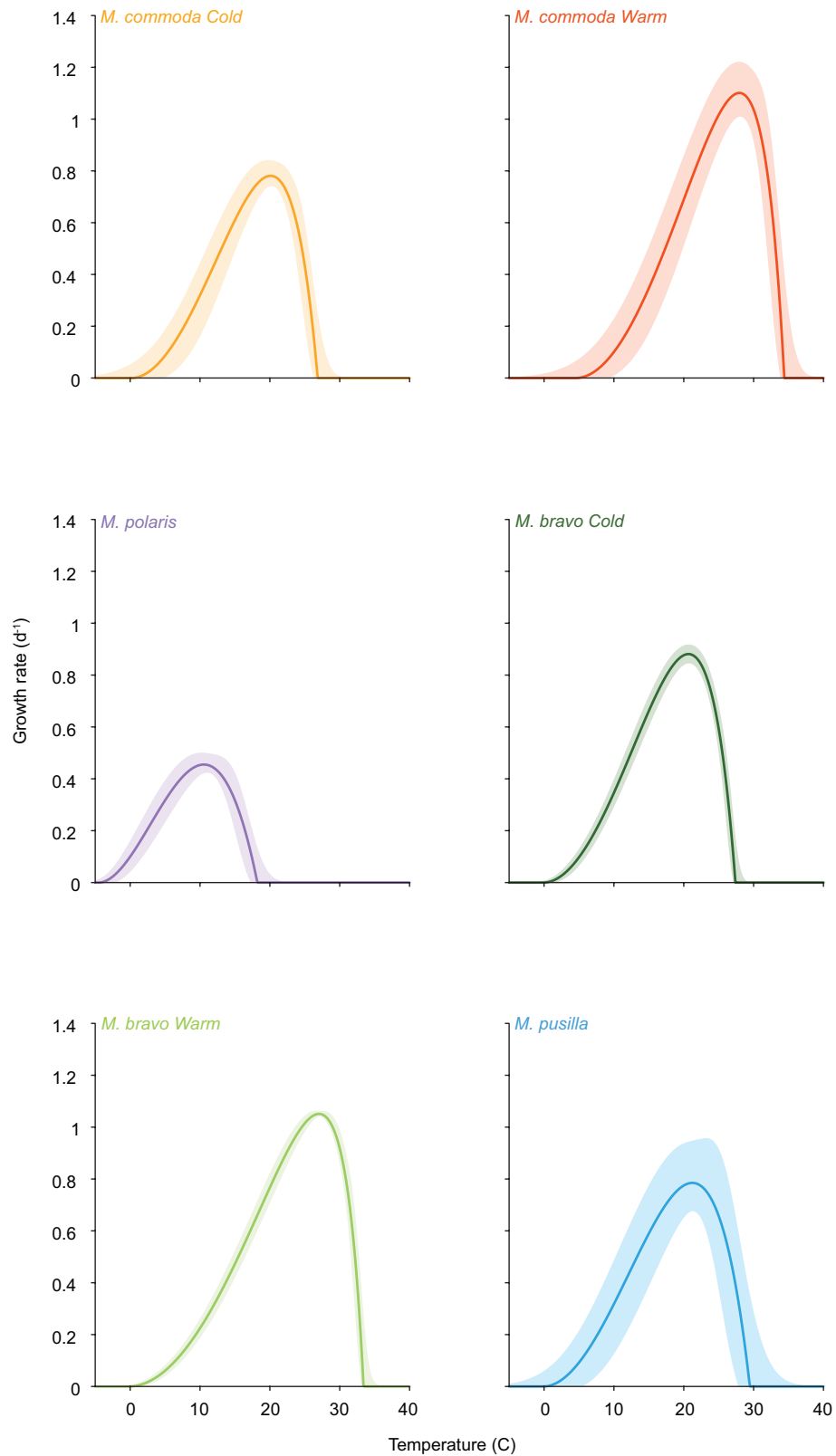
Supplementary Figure 8: Linear relationship between the maximal temperature of growth (T_{max}) and the optimal temperature of growth (T_{opt}) for the eleven strains tested experimentally. The star on top of the vertical axis represents a statistically significant relationship ($p\text{-value} < 0.05$).



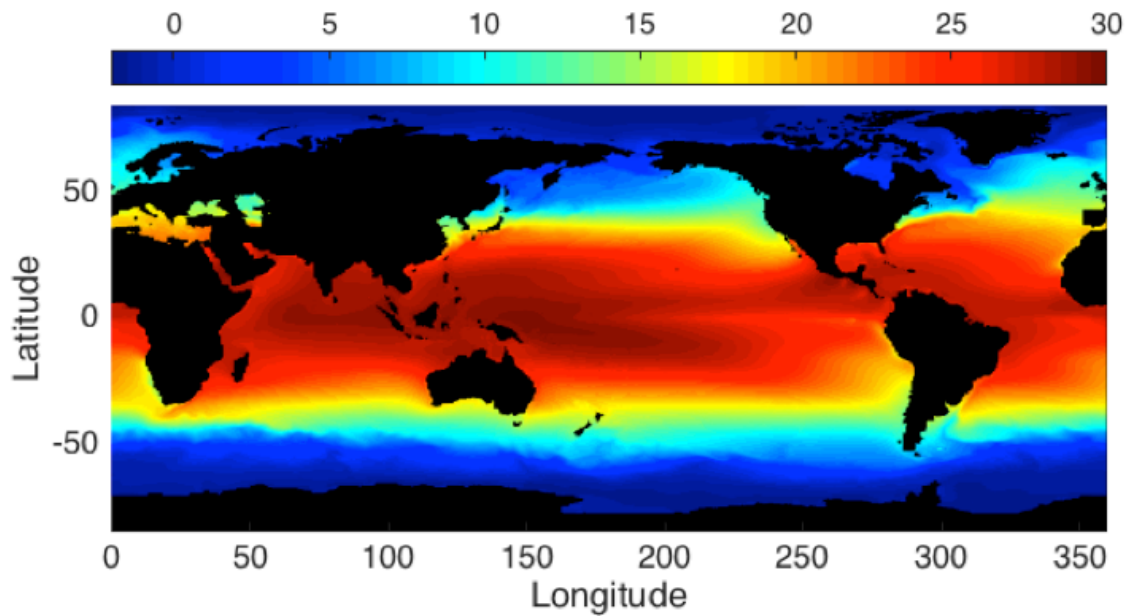
Supplementary Figure 9: Boxplot of cardinal parameters (T_{min} , T_{max} and T_{opt}) and optimal growth rate (μ_{opt}) for the 6 *Micromonas* thermotypes.



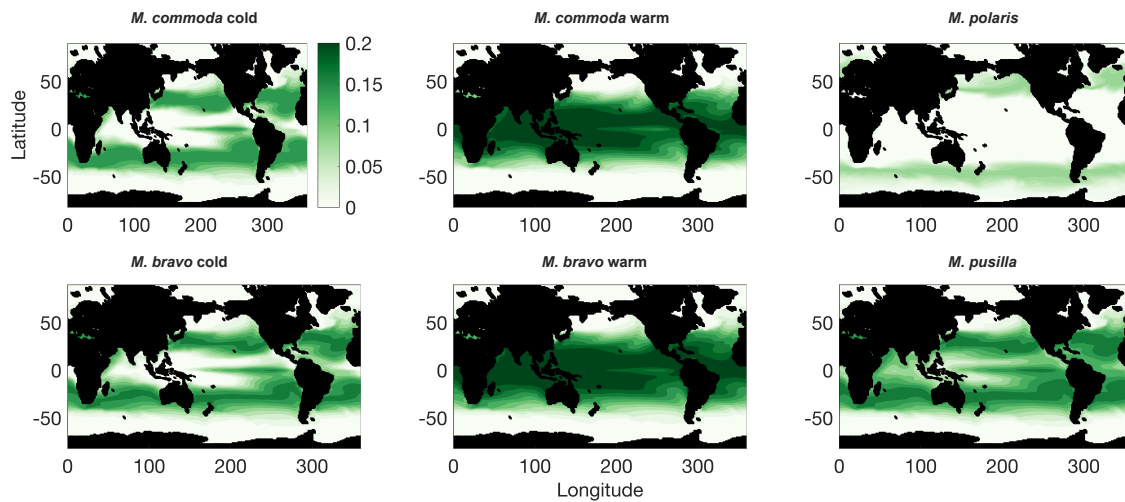
Supplementary Figure 10: Thermal niche width ($T_{max} - T_{min}$) for the six *Micromonas* thermotypes. Error bars represent the standard deviation.



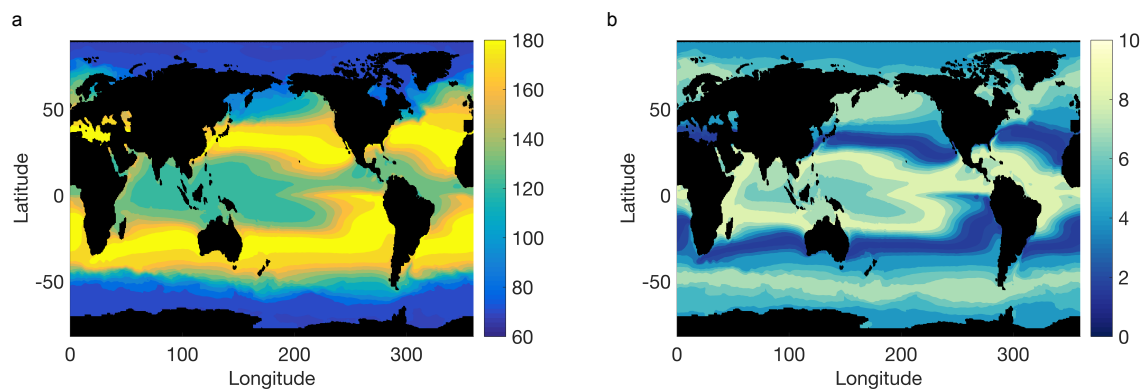
Supplementary Figure 11: Average thermal response of the six *Micromonas* thermotypes (solid lines) within their associated 95% confidence interval (shaded area).



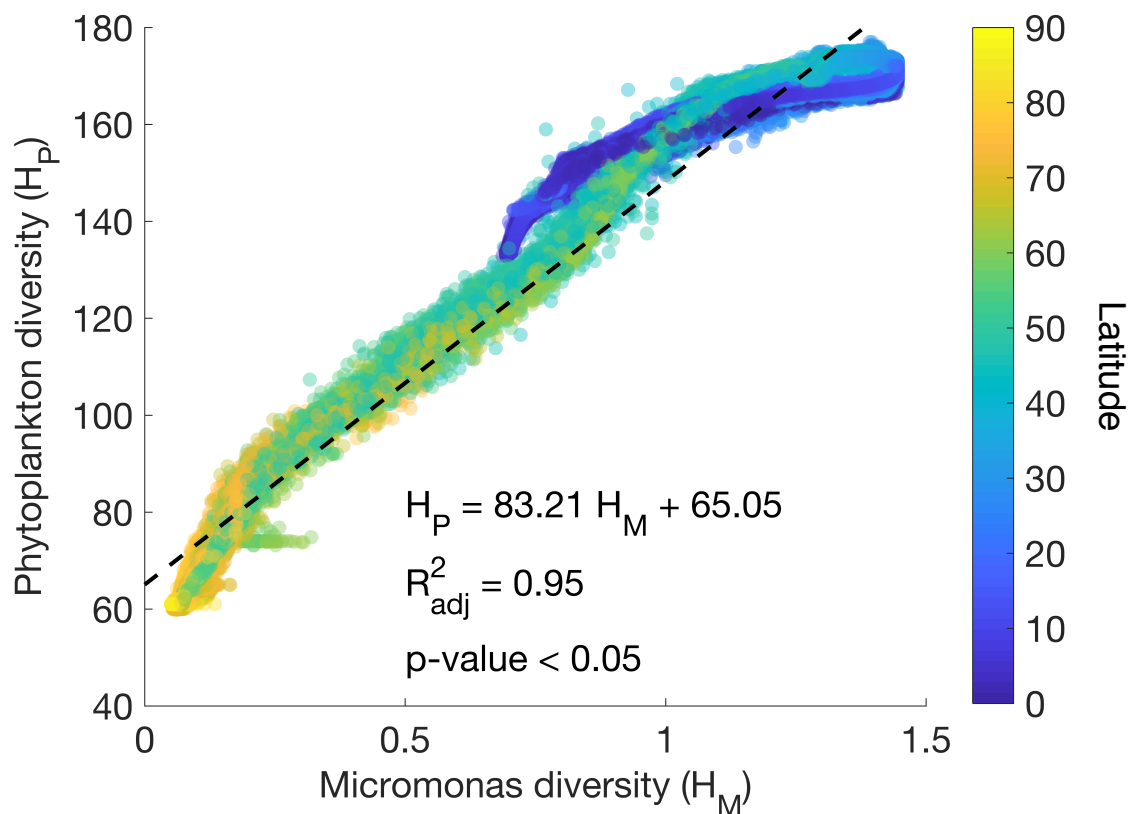
Supplementary Figure 12: Annual average SST (°C) from the Copernicus Marine Service Monitoring for the period 2005 to 2014.



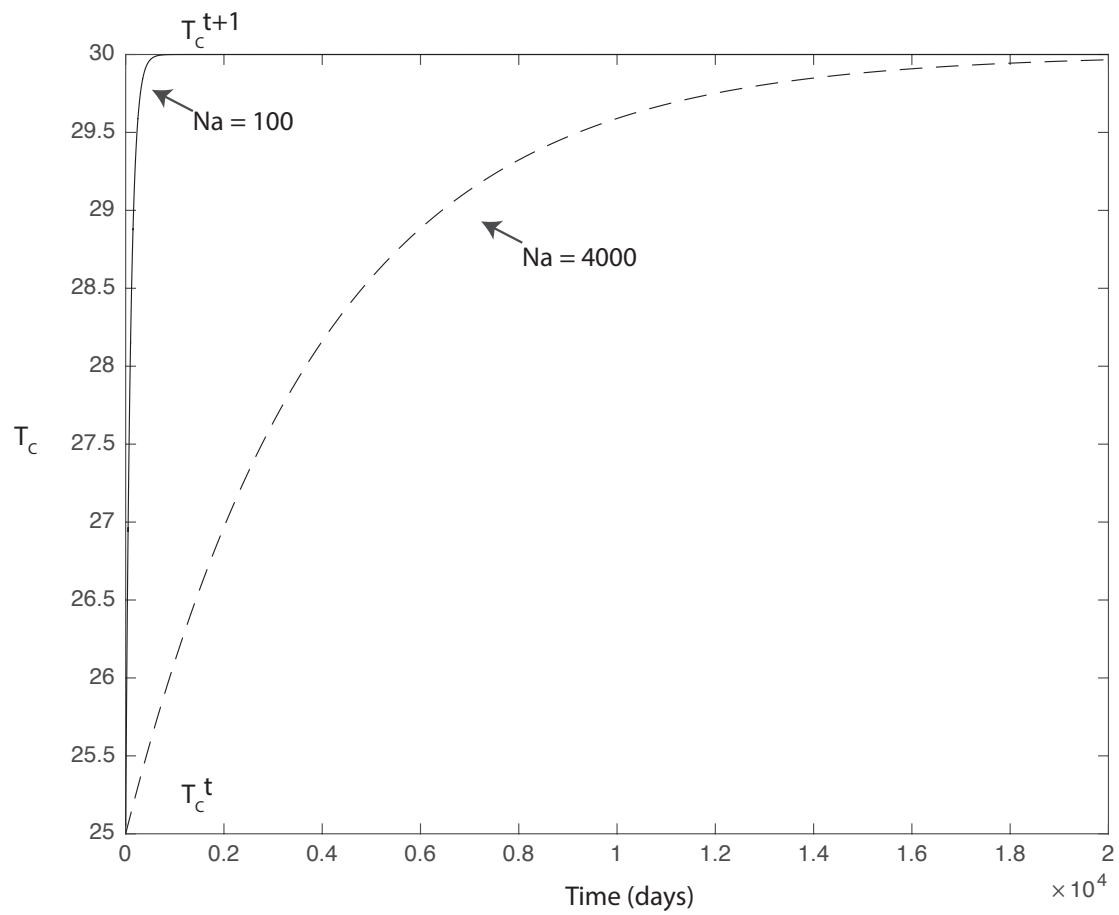
Supplementary Figure 13: Average distribution of the six *Micromonas* thermotypes over the period 2005-2014. The color-bar represents the distribution index $D_i = \frac{\mu_i(T)}{\sum \mu_{opt,i}}$ depending on the global SST from the Copernicus Marine Service Monitoring.



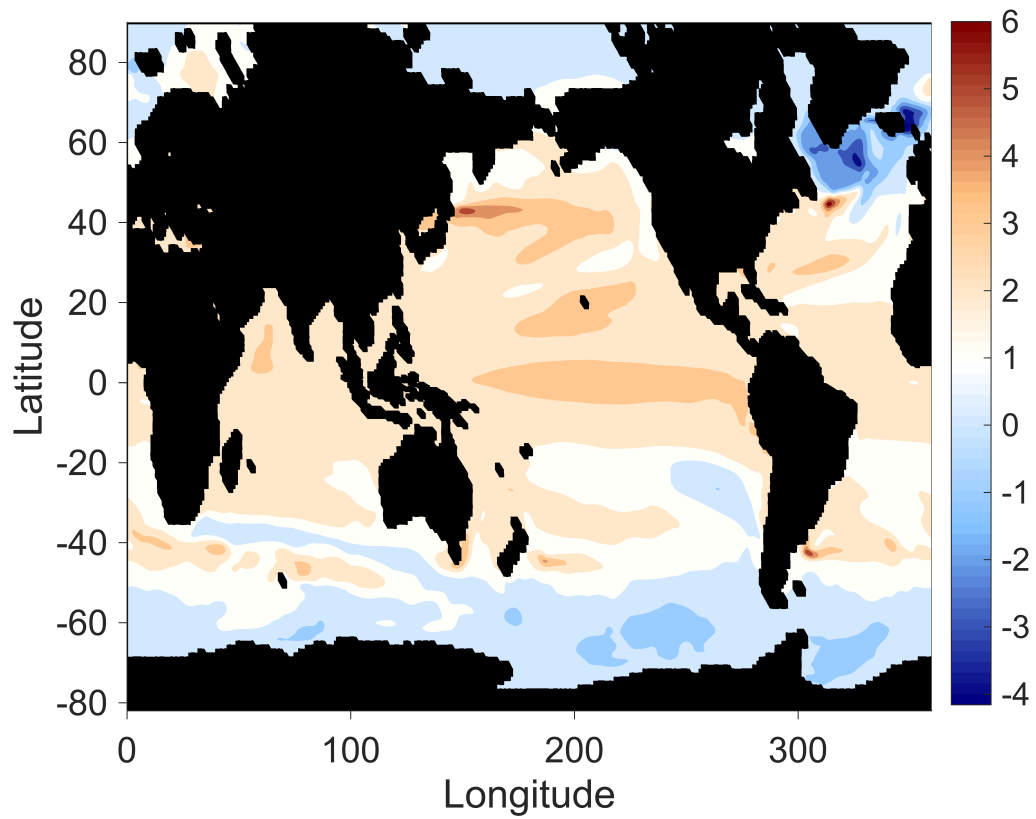
Supplementary Figure 14: Statistics of the *Micromonas* diversity calculated according to 10,000 set of parameters for the 6 thermotypes. (a) Global average diversity. (b) Standard error of the mean expressed as the % difference with the average diversity.



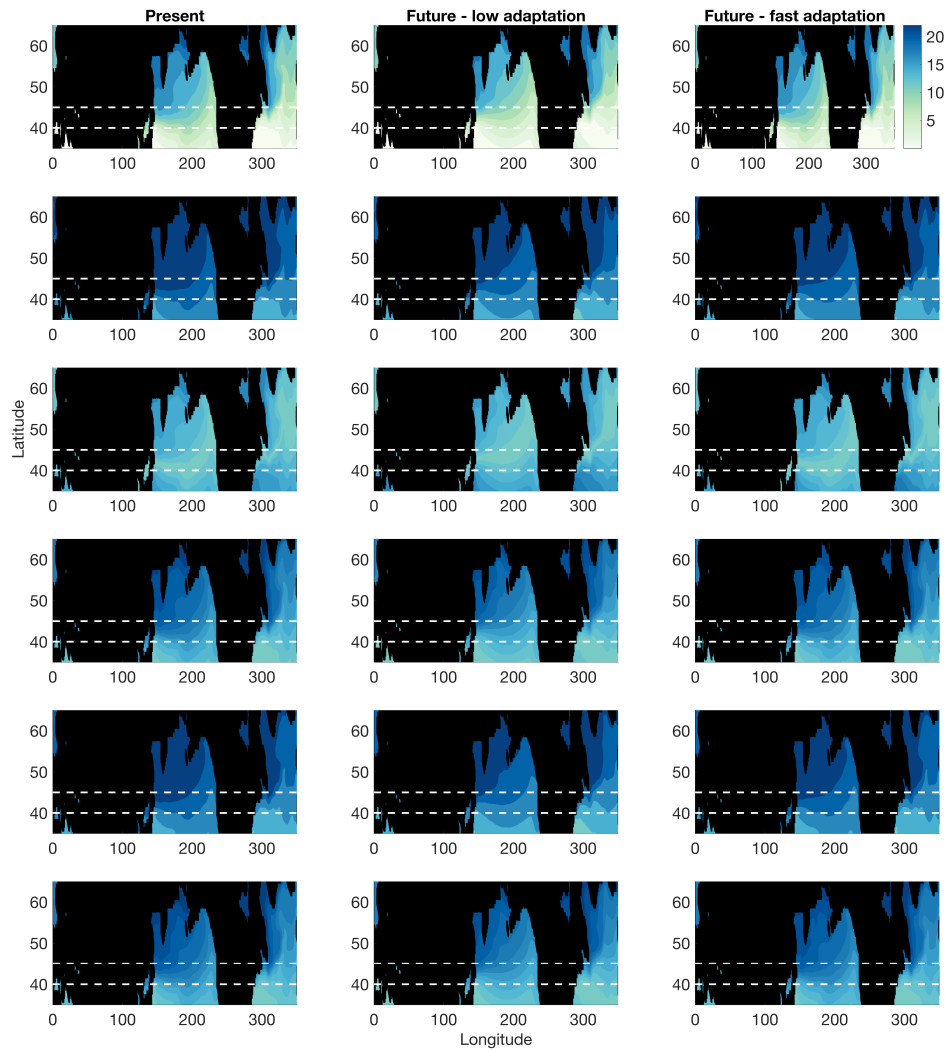
Supplementary Figure 15: Linear relationships between phytoplankton diversity (H_T - [9]) and *Micromonas* interspecific diversity (H_M - present study).



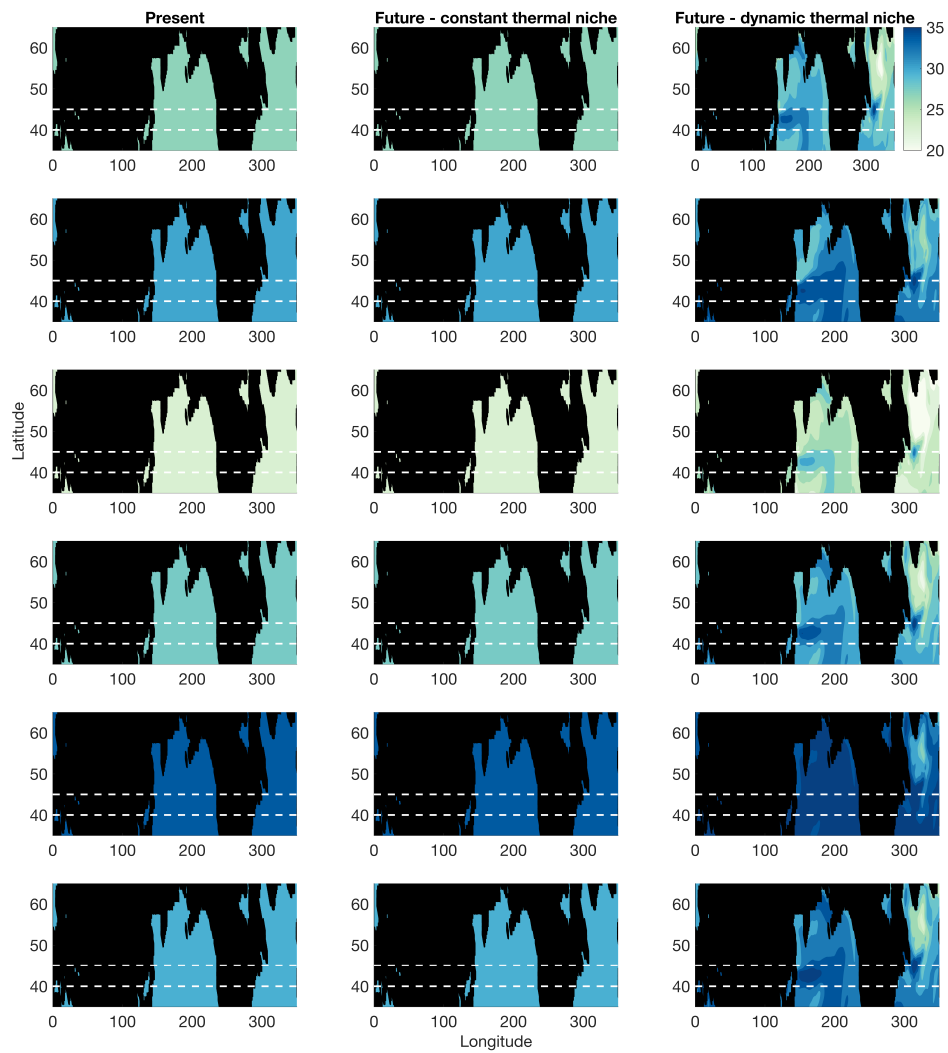
Supplementary Figure 16: Example of evolution of cardinal parameters with the dynamical model (eq. 2 in the main manuscript). Here we presented the generic cardinal parameter T_C (T_{min} , T_{opt} , T_{max}) between time t (T_C^t) and time $t + 1$ (T_C^{t+1}) for two evolution time scales: fast ($Na = 100$ generations) and slow ($Na = 4000$ generation).



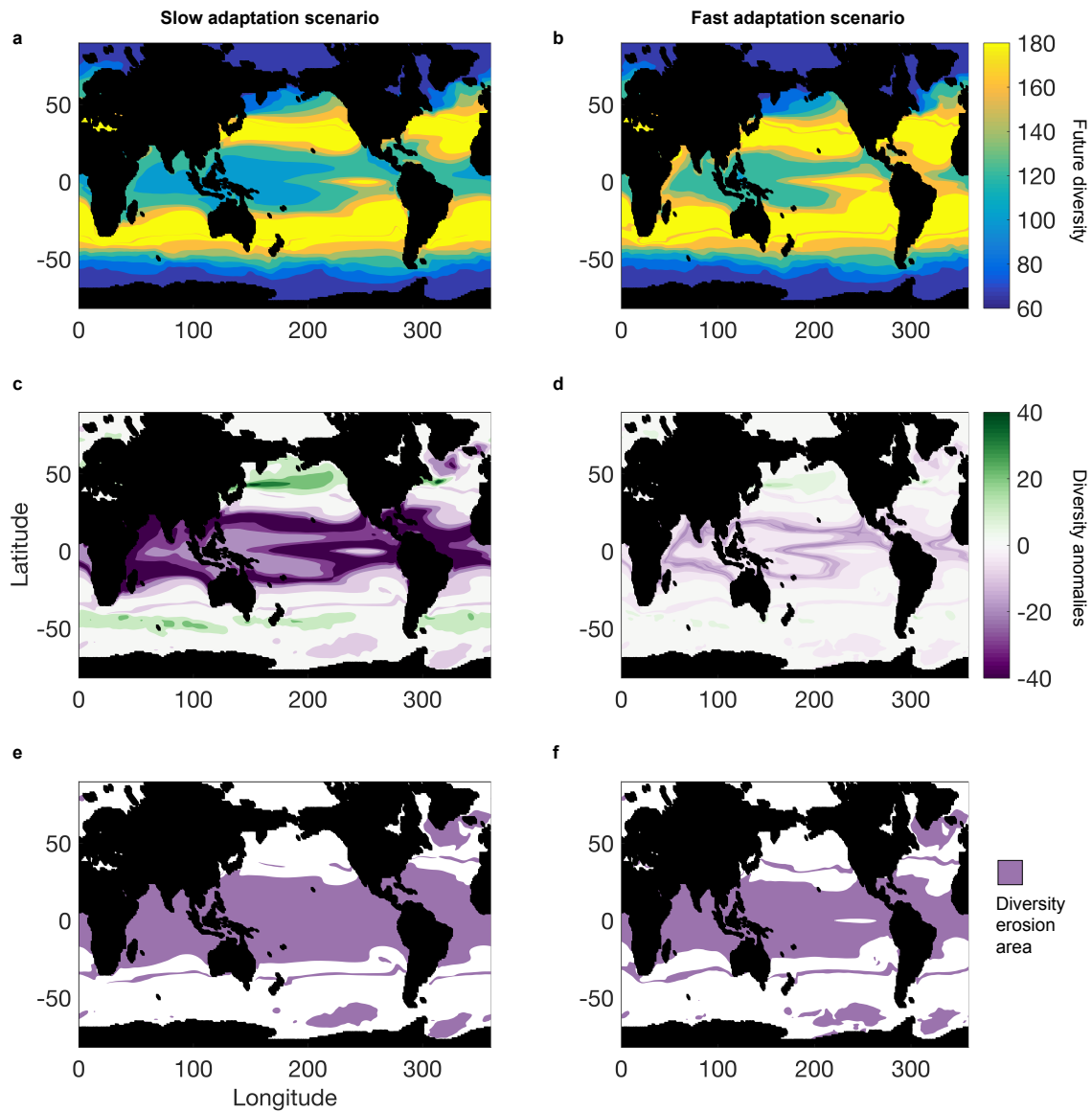
Supplementary Figure 17: *SST anomalies between the present (2001-2010) and future (2091-2100) periods. Projections of global future temperature regimes were obtained from the NOAA GFDL CM2.1 [10, 11] driven with the SRES A2 emissions scenario [12].*



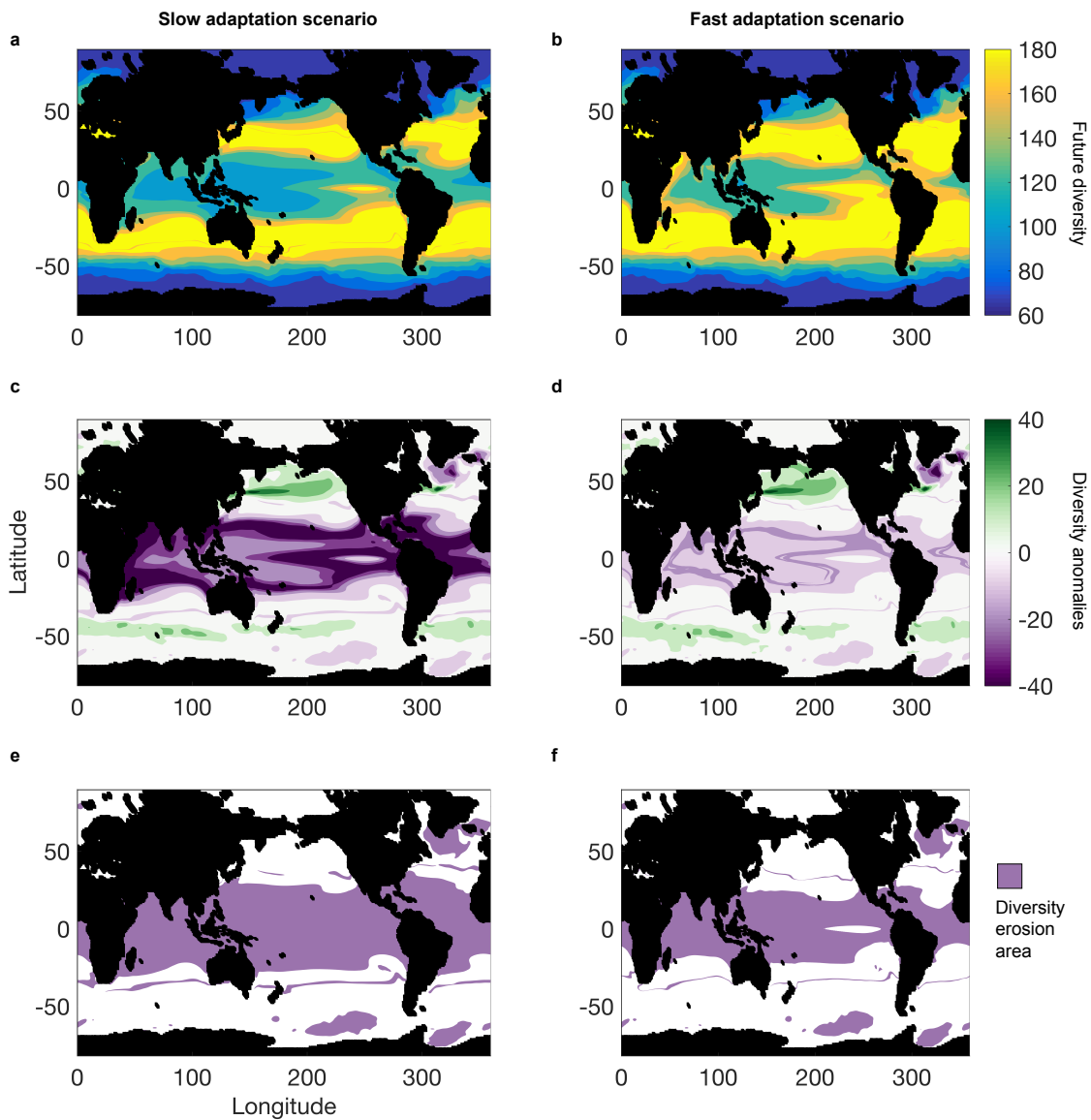
Supplementary Figure 18: Comparison of the index $|T_{opt} - \overline{T_S}|$ for the hypothesis Specialist-generalist with constant thermal niche for slow and fast adaptation scenarios. Low values indicate that T_{opt} is close to $\overline{T_S}$. The maps are centered on the 35-65°N. White dashed lines represent the 40-45°N zone where we observed a diversity gain related to an increase in temperature in the future.



Supplementary Figure 19: Comparison of the thermal niche ($T_{max} - T_{min}$) for the fast scenario ($N_a = 100$) for two hypotheses: Specialist-generalist with constant thermal niche and with dynamic thermal niche. The maps are centered on the 35-65°N. White dashed lines represent the 40-45°N zone where we observed a diversity gain related to an increase in temperature in the future.



Supplementary Figure 20: *Evolution of diversity for two different scenarios of adaptation kinetic (a,c,e. $N_a = 100$ and b,d,f. $N_a = 10^6$) between the present (2001-2010) and the future (2091-2100) periods with the Specialist-generalist hypothesis with constant thermal niche. (a-b) Future diversity. (c-d) Diversity anomalies calculated as the difference between future and present diversity. (e-f) Diversity erosion area represent the area where the anomalies are negatives.*



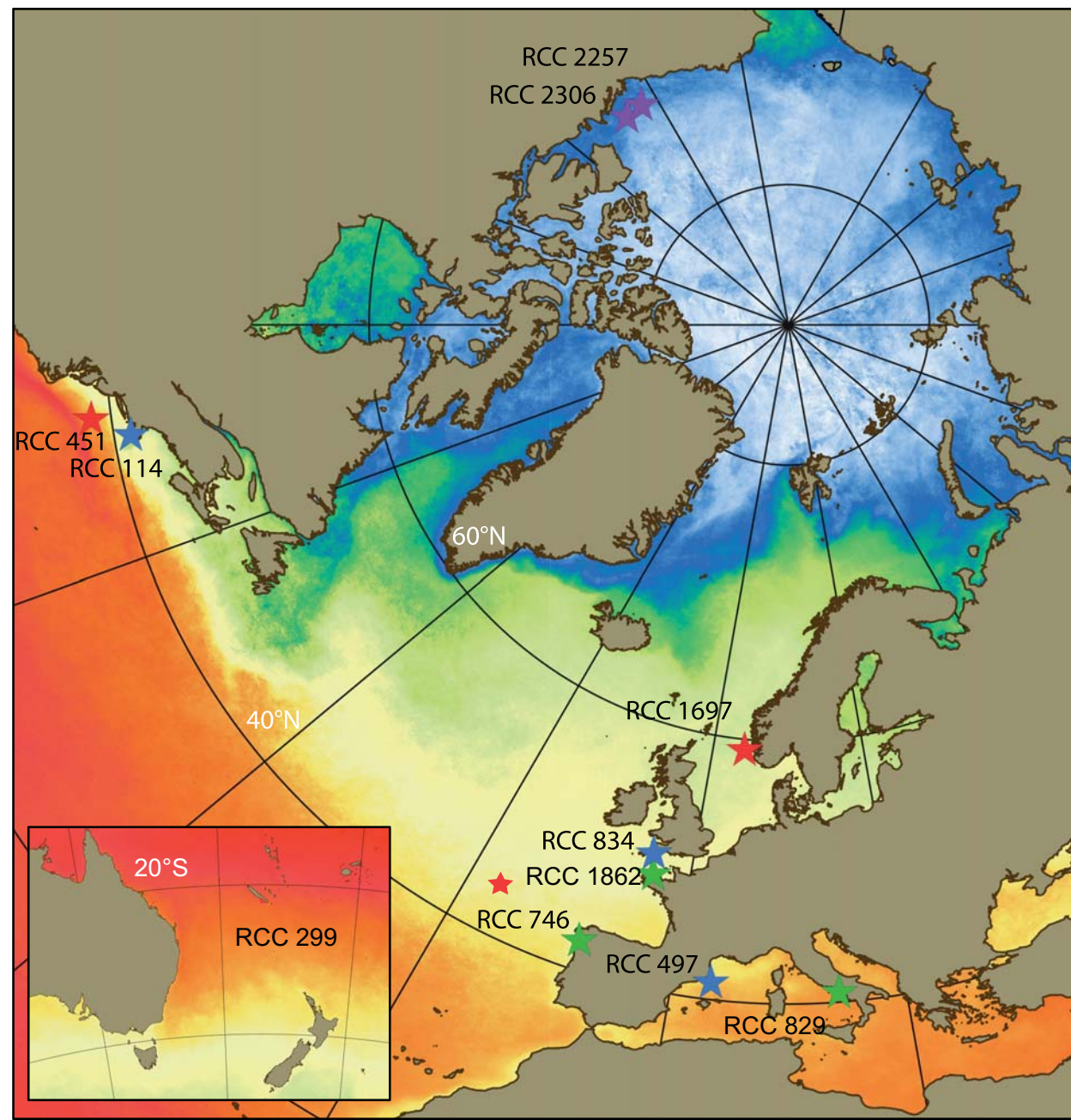
Supplementary Figure 21: *Evolution of diversity for two different scenarios of adaptation kinetic (a,c,e. $N_a = 100$ and b,d,f. $N_a = 10^6$) between the present (2001-2010) and the future (2091-2100) periods with the Specialist-generalist hypothesis with dynamic thermal niche. (a-b) Future diversity. (c-d) Diversity anomalies calculated as the difference between future and present diversity. (e-f) Diversity erosion area represent the area where the anomalies are negatives.*

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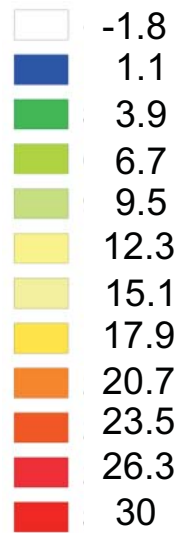
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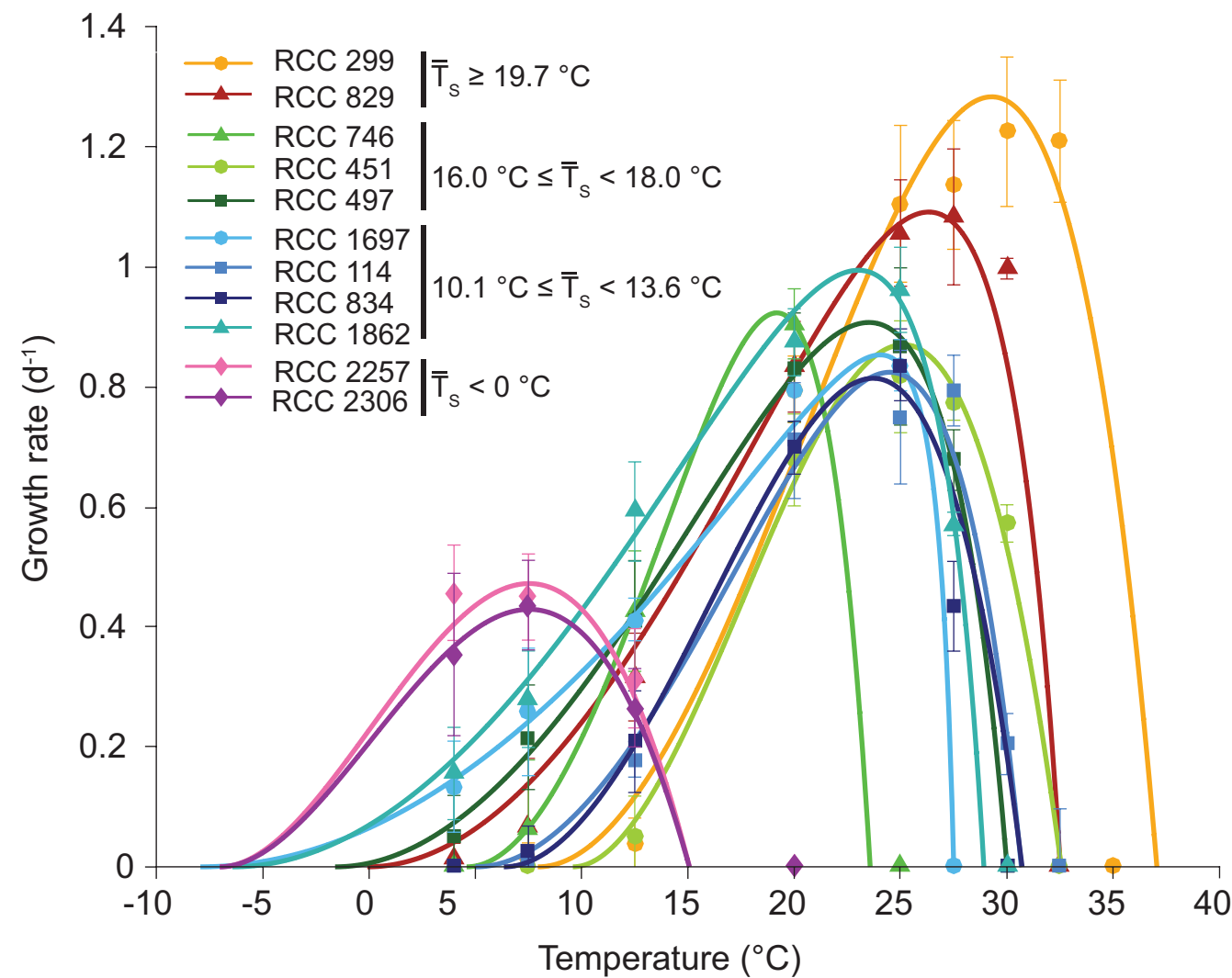
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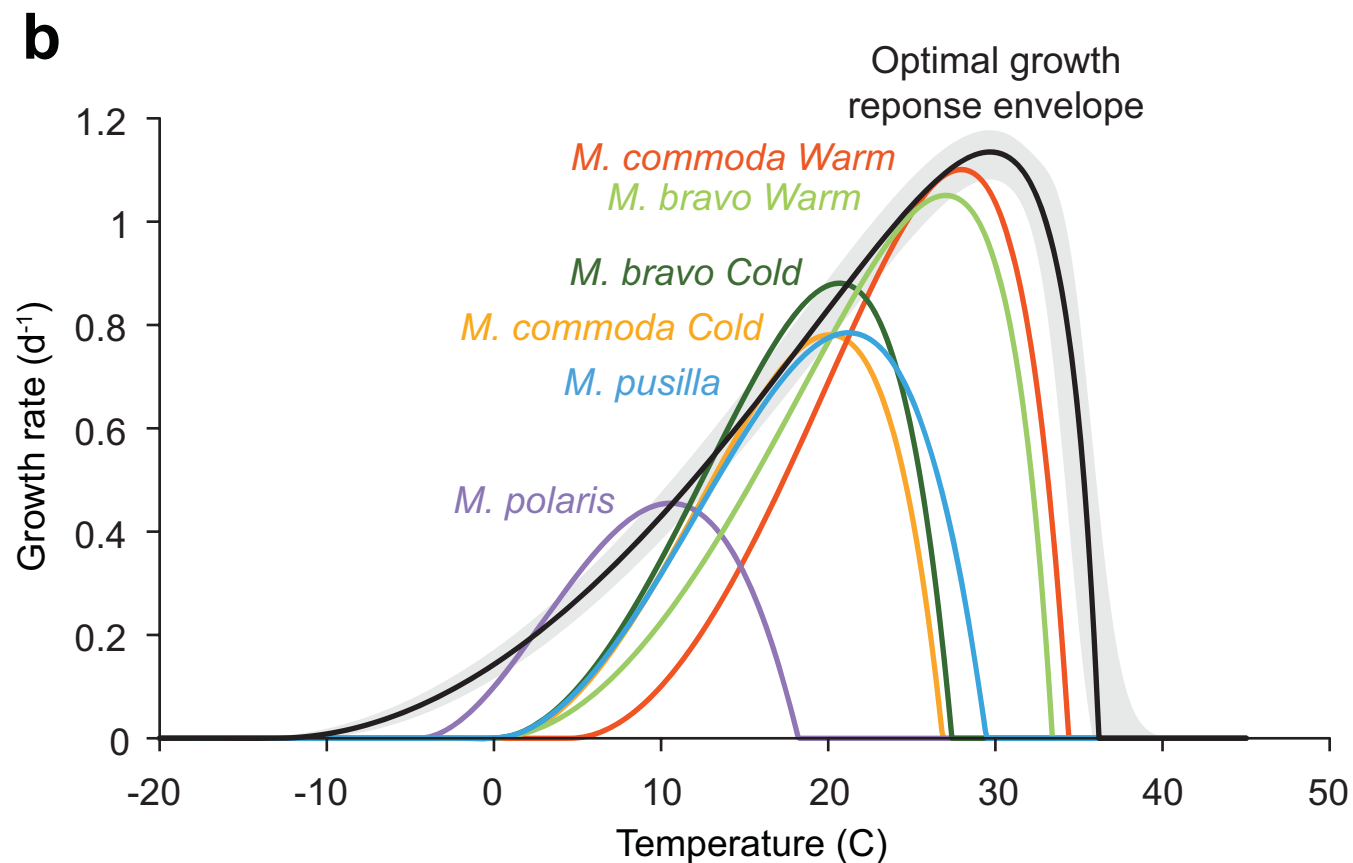
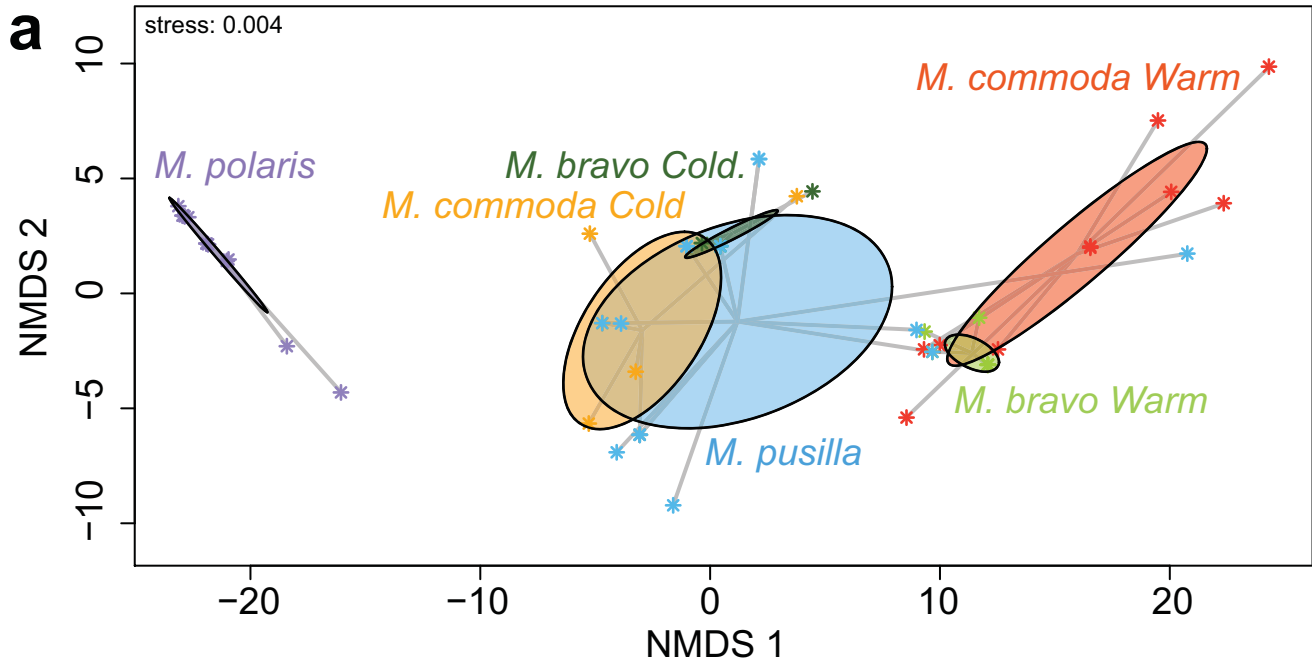


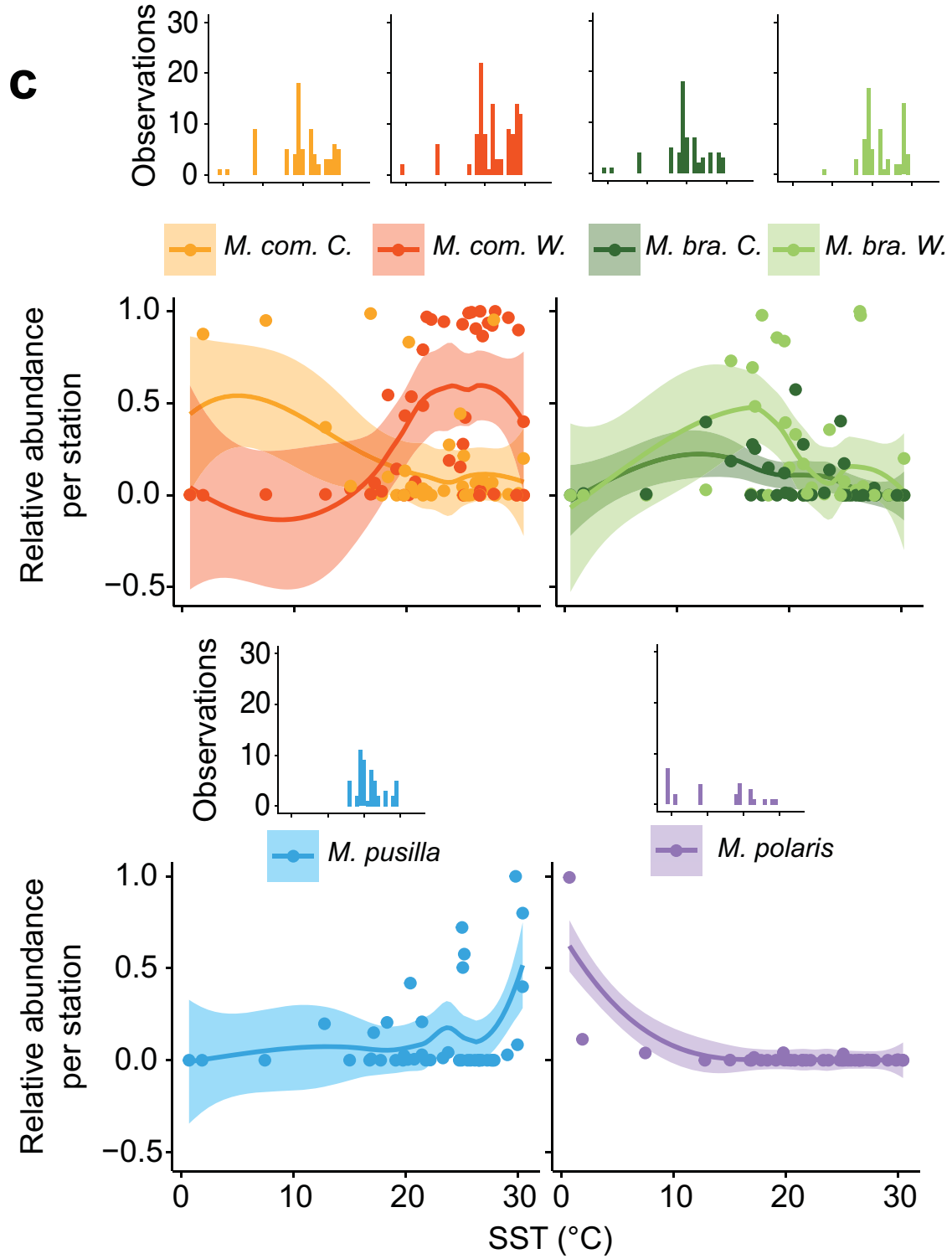
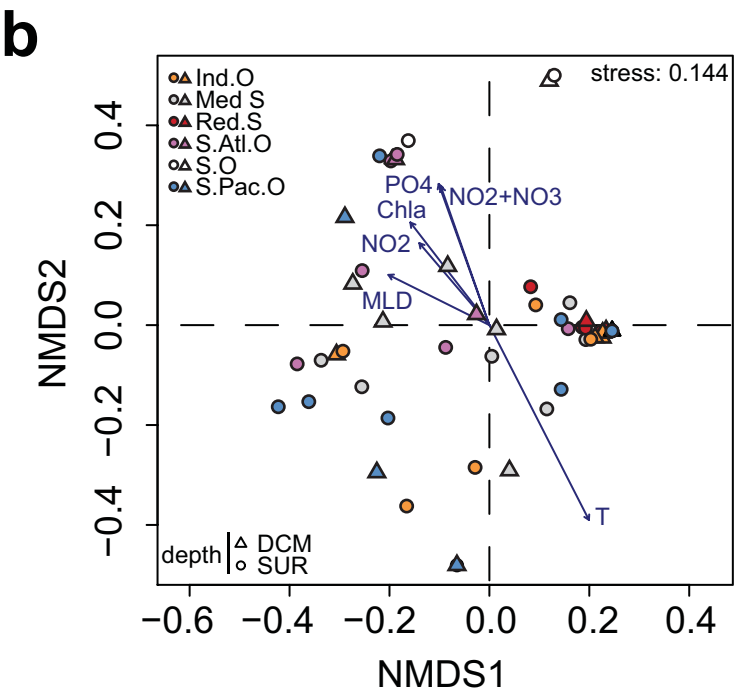
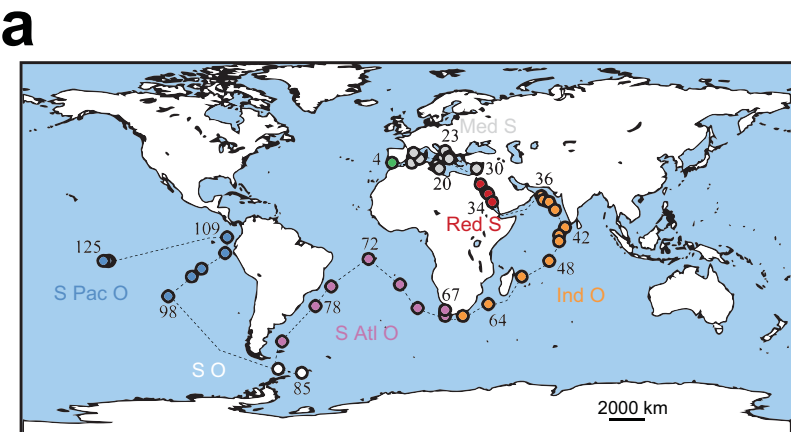
Micromonas Species

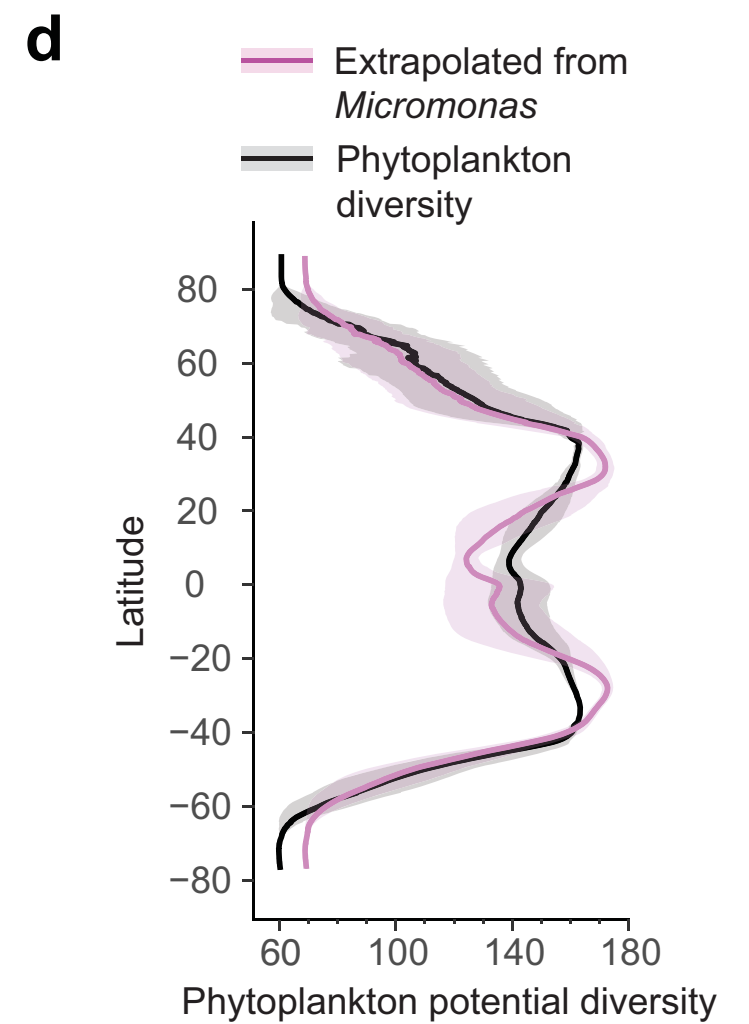
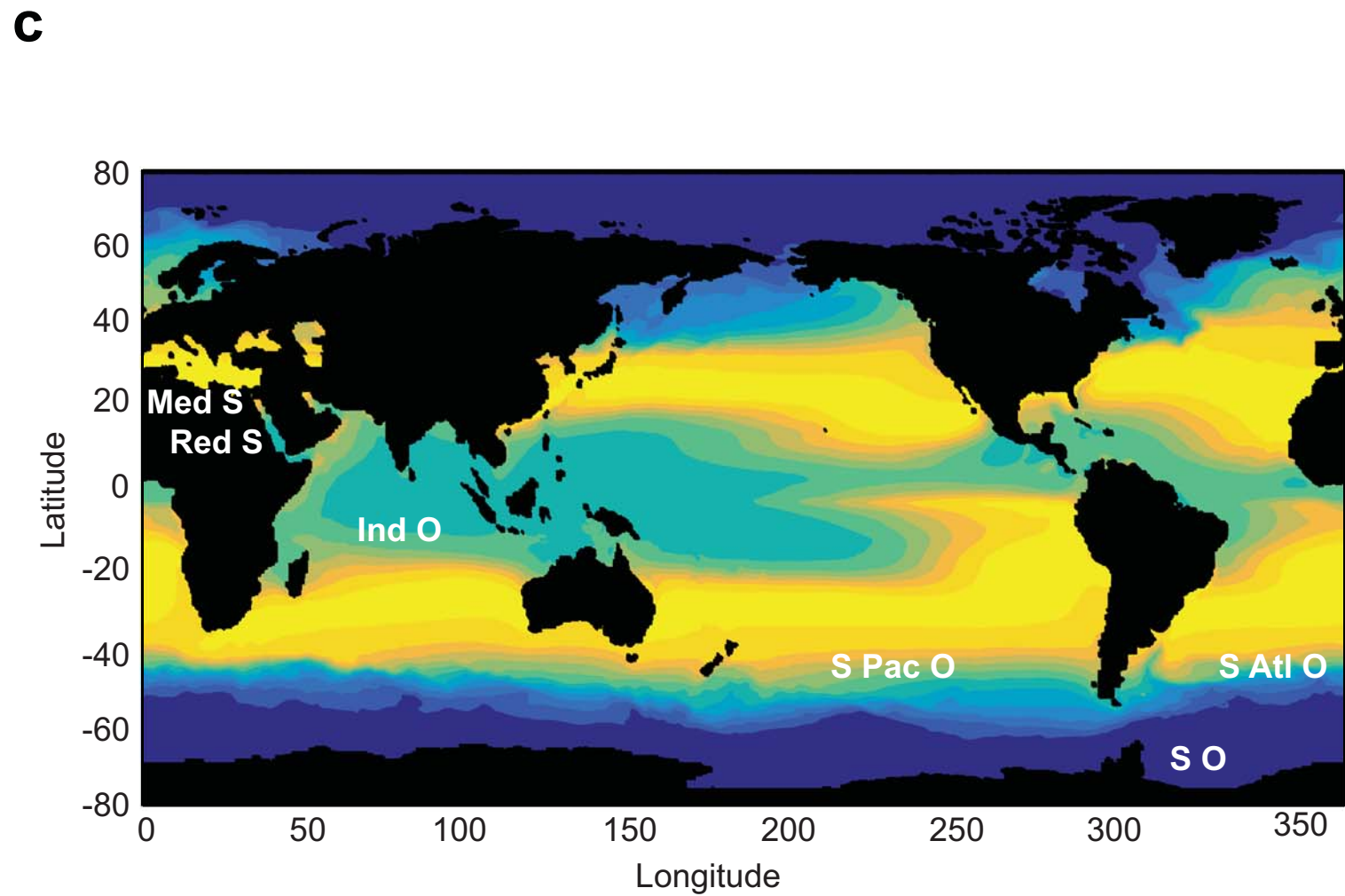
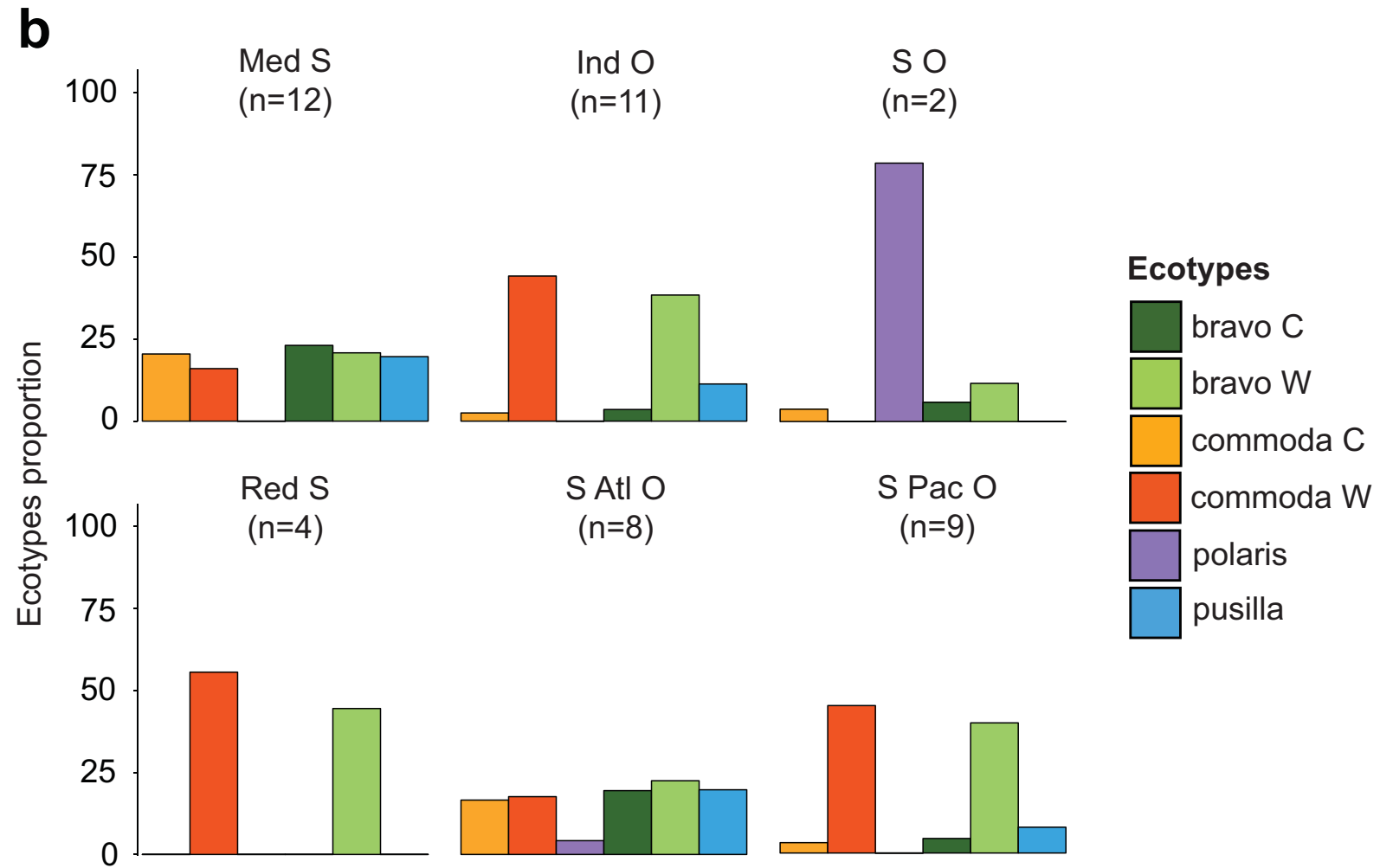
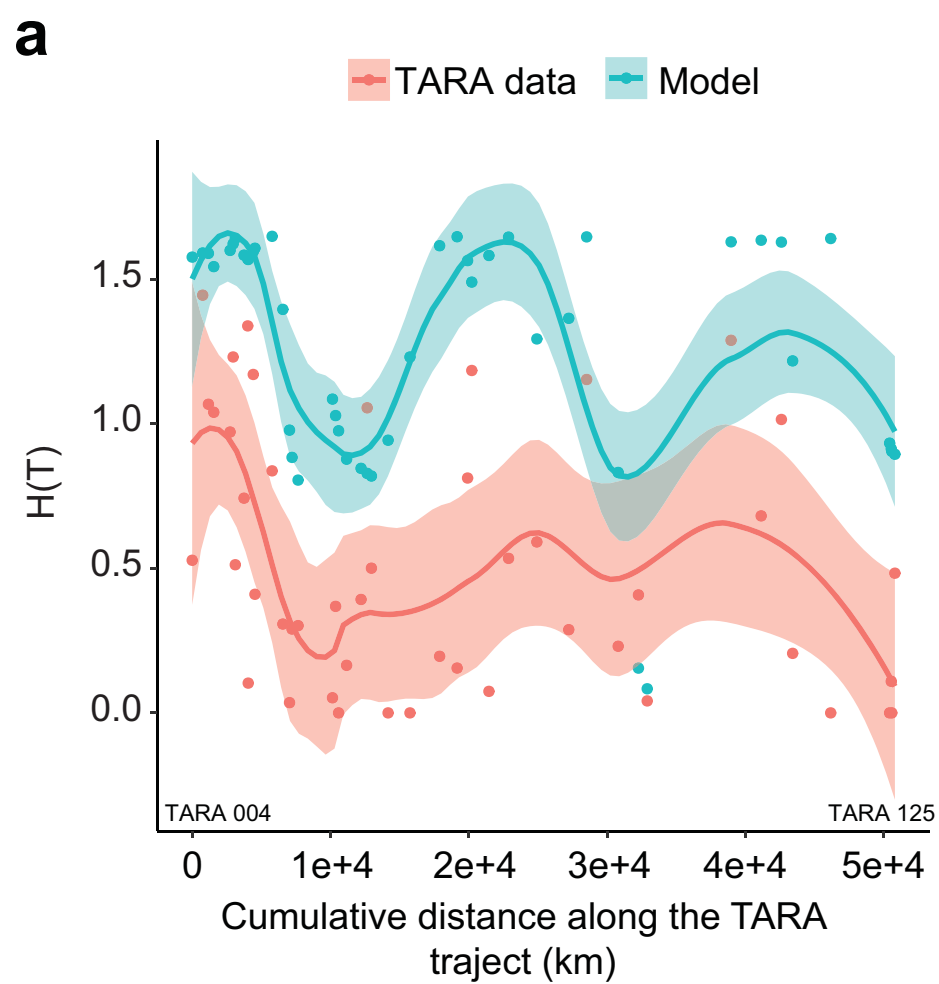
- ★ *M. pusilla*
- ★ *M. bravo*
- ★ *M. polaris*
- ★ *M. commoda*

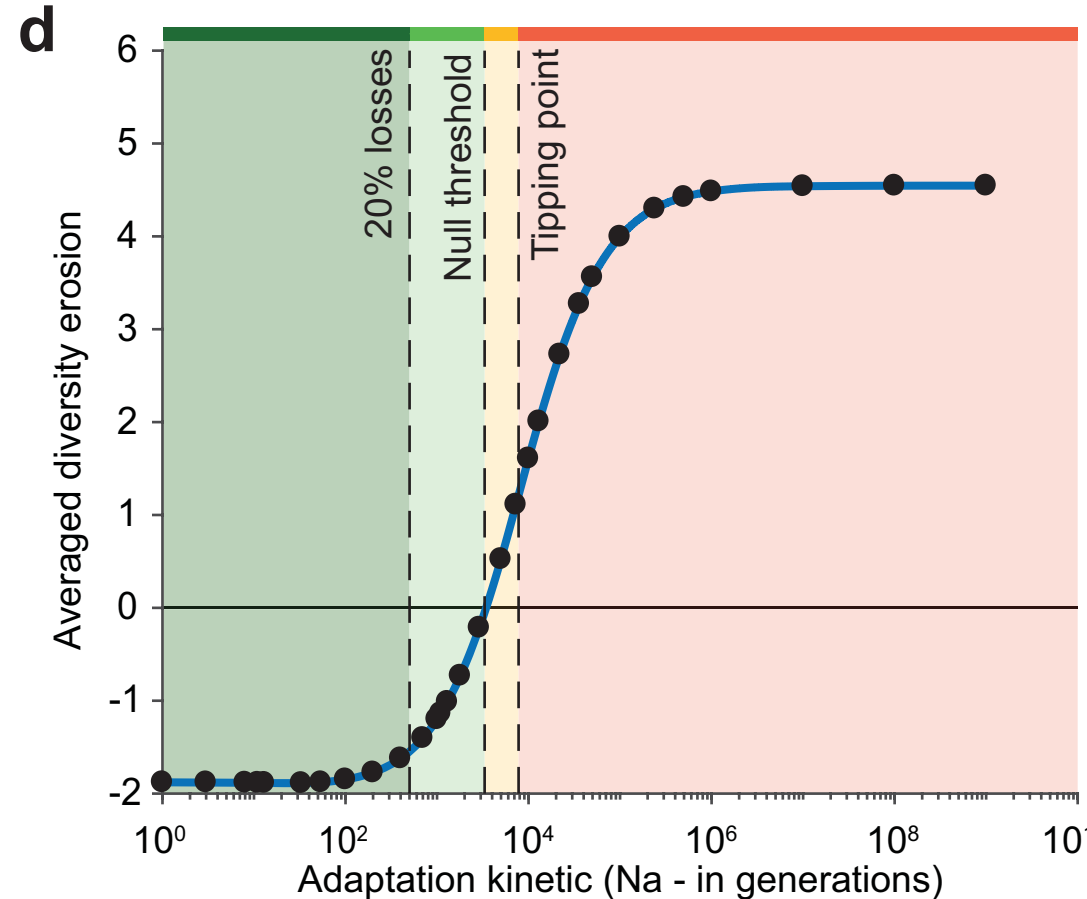
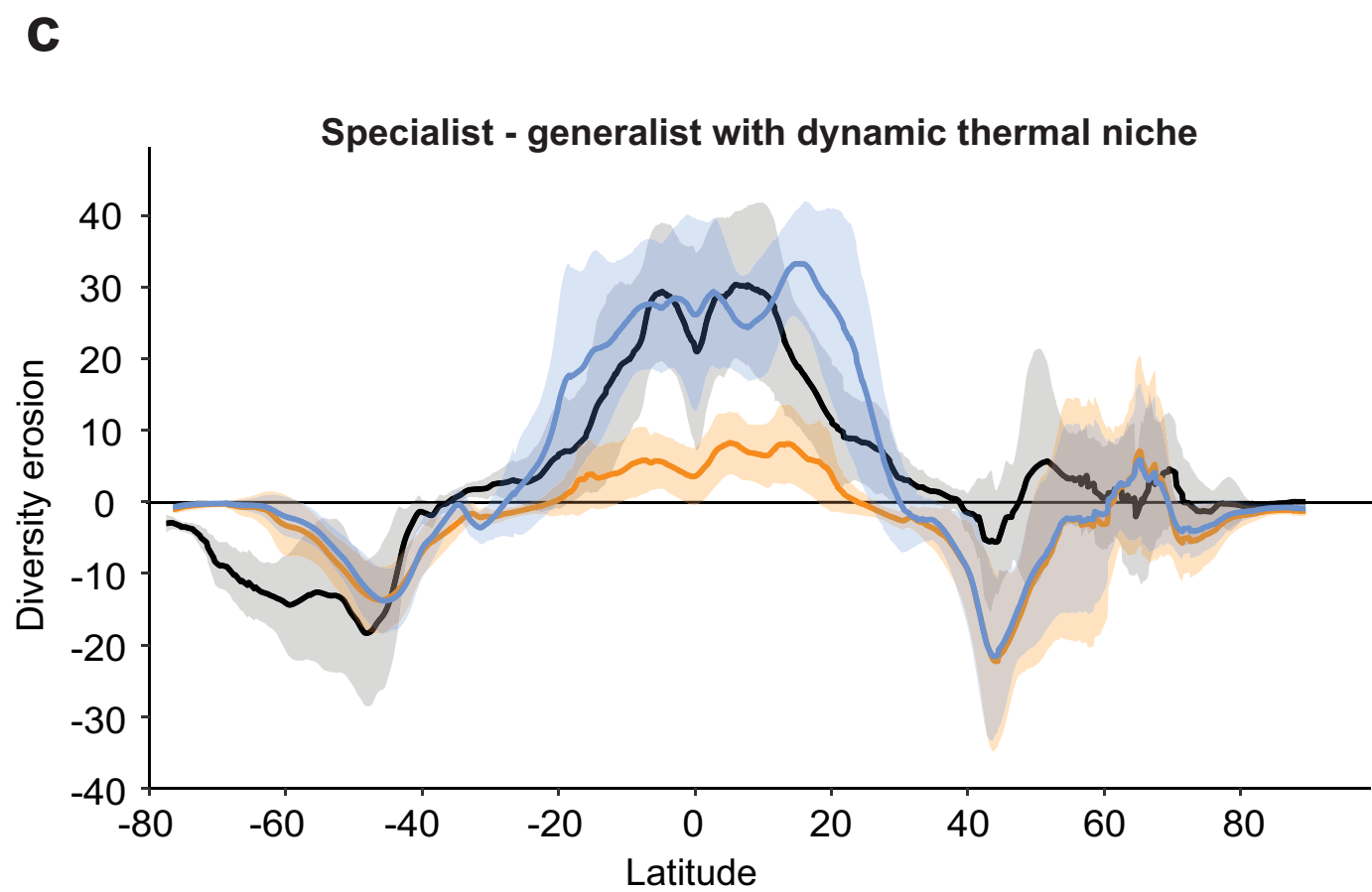
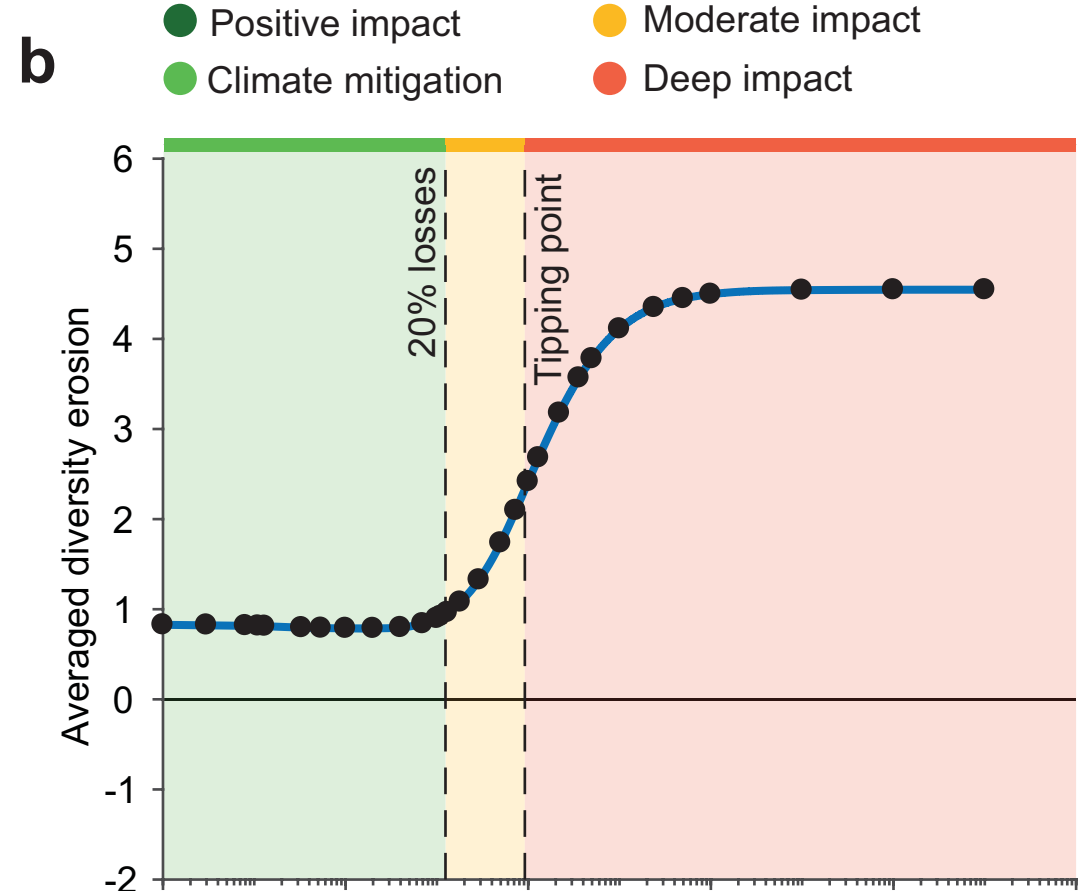
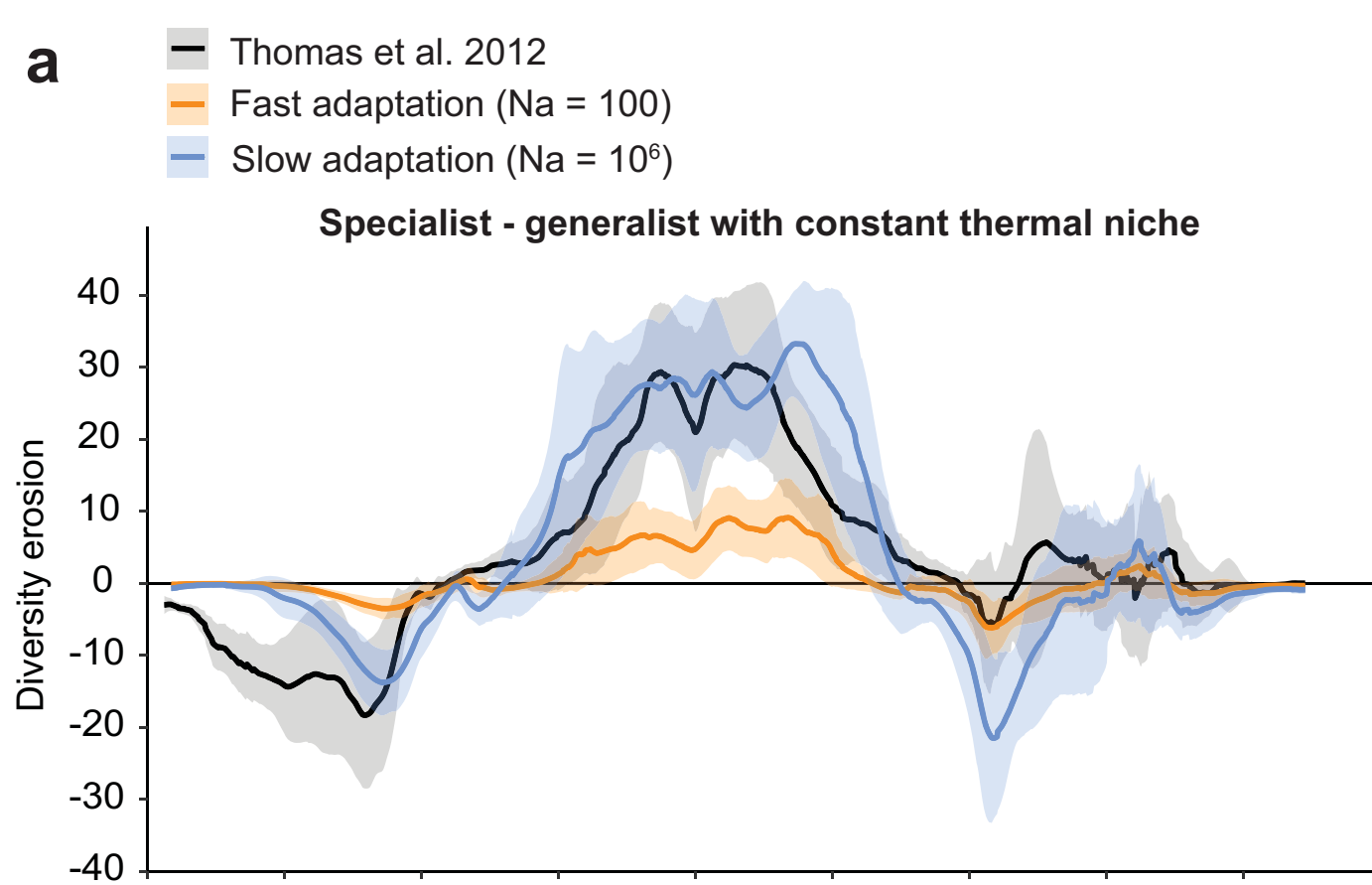
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Cardinal Parameter	Model	R² adjusted	p-value
μ_{opt}	$\mu_{opt} = 0.03\bar{T}_S + 0.47$	0.90	$5.68 \cdot 10^{-6}$
T_{max}	$T_{max} = 0.77\bar{T}_S + 17.73$	0.79	0.00014
T_{opt}	$T_{opt} = 0.84\bar{T}_S + 10.24$	0.79	0.00015
T_{min}	$T_{min} = -0.76Lat - 0.92\bar{T}_S + 49.33$	0.47	0.03