Functional redundancy in natural pico-phytoplankton communities depends on temperature and biogeography

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Abstract:

Biodiversity affects ecosystem function, but how this relationship will pan out in a changing world is still a major question in ecology. It remains especially understudied for pico-phytoplankton communities, which contribute to carbon cycles and aquatic food webs year-round. Observational studies show a link between phytoplankton community diversity and ecosystem stability, but there is only scarce causal or empirical evidence. Here, we sampled phytoplankton communities from two biogeographically distinct (but close enough to not be confounded by differences in day length and precipitation) regions in the Southern Baltic Sea, and carried out a series of dilution/regrowth experiments across three assay temperatures. This allowed us to investigate the effects of loss of rare taxa and establish causal links in natural communities between species richness and several ecologically relevant traits (e.g. size, biomass production, and oxygen production), depending on sampling location and assay temperature. We found that the samples' bio-geographical origin determined whether and how functional redundancy changed as a function of temperature for all traits under investigation. Samples obtained from the slightly warmer and more thermally variable regions showed overall high functional redundancy. Samples from the slightly cooler, less variable, stations showed little functional redundancy, i.e. function decreased the more species were lost from the community. The differences between regions were more pronounced at elevated assay temperatures. Our results imply that the importance of rare species and the amount of species required to maintain ecosystem function even under short-term warming (e.g. during heat waves) may differ drastically even within geographically closely related regions of the same ecosystem.

Key words: Functional redundancy, global warming, pico-phytoplankton communities, Baltic Sea

Introduction

When ecosystems lose species, the function and services of the ecosystem may decline. The insurance hypothesis states that ecosystem stability increases with biodiversity [1]. Evidence has long been emerging for this to be true across taxa and biomes, spanning heterotrophic and autotrophic microbial communities to plants to metazoans, i.e. ecosystems with higher biodiversity tend to be more productive on average regardless of the type of organism under investigation [2-6]. In a warming world, variation in temperature may shape the biodiversity-ecosystem function relationship on short and long-term time scales [7,8]. A recent study has experimentally examined the synergistic effects of warming and biodiversity loss on function in bacterial assemblages [9], but no comparable data exist for natural phytoplankton communities. As a consequence, studies on phytoplankton biodiversity and ecosystem function remain largely observational [2] and usually do not consider loss of biodiversity in interaction with aspects of climate change (but see [10]) or evolutionary history (but see [11] for population genetics). Pico-phytoplankton contribute about 20% of phytoplankton primary production [12], and unlike larger phytoplankton, they do not form blooms, but contribute to the photosynthesising foundation of aquatic ecosystems all year [13,14]. They show rapid physiological [15,16] and evolutionary [17,18] responses to changing environments when studied as single-strain cultures. There is isolated evidence that the speed and mechanism of evolutionary responses in a changing environment may differ between phytoplankton strains evolving in isolation and strains evolving in communities, mixed cultures, or multi-genotype biofilms [19-23]. Comparable experiments have not been carried out for pico-phytoplankton (but see [24]). As a consequence, we need to conduct manipulative experiments to establish a better understanding of how the links between pico-phytoplankton community function and pico-phytoplankton community diversity change with temperature on short- and long-term timescales. Since natural phytoplankton strains are notoriously difficult to grow in isolation

68   under laboratory conditions, assembling artificial communities from natural phytoplankton

69   components can be an arduous task. Organisms from culture collections which have already

70   been shown to grow well in isolation are easier to assemble into communities (e.g.[10]) but

71   may not reflect well the complex environments that the lineages were originally sampled from.

72   Therefore, when working with natural assemblages, serial dilution of natural samples can

73   provide a useful tool to reduce biodiversity to such an effect that rare species are lost, and

74   common species remain [25,26].

75

76   Here, we investigated the combined effects of transient warming and biogeographic history on

77   the diversity-function relationship in natural pico-phytoplankton communities. To do so, we

78   obtained pico-phytoplankton community samples during two cruises of RV ALKOR (AL505

79   and AL507) on the Southern Baltic Sea in 2018 (see Figure 1 and Table S1). Of the two basins

80   sampled, the Kiel Bight is characterised by, on average 2 ºC higher temperature than the

81   Bornholm Basin and unpredictable fluctuations in temperature on the timescale of days to

82   months (Santelia *et al.* in prep – SI document 2). In the Bornholm Basin, fluctuations in

83   temperature follow a highly predictable pattern governed by seasonality (Santelia *et al.* in prep

84   – SI document 2). The basins are connected through currents [27], and the regions are

85   geographically close to each other (see Figure 1) so that we can rule out confounding effects

86   introduced by e.g. differences in precipitation, day length ,and light intensity [28]. By assaying

87   the effect of species loss on communities across three temperatures within the range of

88   Southern Baltic Sea spring and summer temperatures [27,28], we can test the contributions of

89   long-term (comparison of basins) and short-term (assay temperatures) changes in temperature

90   on key community functions.

91

92

93   **Methods**

94   **This is a methods summary. The full methods are available in the supporting**

95   **information.**

96   We obtained pico-phytoplankton community samples during two RV ALKOR cruises

97   (AL505 and AL507 respectively) in 2018 (see Figure 1 and Table S1 for sampling dates and

98   locations) from 5m. Samples were size fractioned to obtain the pico-phytoplankton

99   community. To rule out effects of parameters other than temperature and diversity during the

100   experiment, all samples were grown in f/2 media [29] at the salinity of the sampling location.

101   Community samples grew in semi-continuous batch culture in a common garden at 18°C and

102   100 µmol quanta $m^{-2} s^{-1}$ (12:12 light/dark cycle) until used for the experiment. We counted

103   cell numbers in all samples the flow cytometre, and the flow cytometric fingerprints also

104   allow for an estimate of phenotypic diversity or trait-level diversity [30] (based on photo-

105   pigment composition and size [31,]Figure S2 for details). Samples were then diluted in 10-

106   fold dilution steps at the appropriate salinity, down to the lowest point of dilution (in theory

107   containing no more than 1 species or pico-phyoplankton per mL). Six technical replicates of

108   each sample were left to regrow to 10^6 cells mL^{-1} at the assay temperatures of 15ºC, 18ºC,

109   and 22ºC . Then, we re-diluted all samples to the same density and tracked a full growth

110   curve. Cell size was obtained from the flow cytometre to calculate an estimate of pg carbon

111   per mL after [32].

112

113   Net photosynthesis rates were obtained when samples were in exponential phase, on PreSens

114   ® SDR Sensor Dish optodes at 10^5 cells mL^{-1} in the measurement vials and measured oxygen

115   production for 15 minutes in the light, and respiration for 15 minutes in the dark.

116

117   We obtained two measures of biodiversity in our samples. One, following CTAB DNA

118   extractions [33], samples were sent for DNA- meta-barcoding at biome-id, resulting in a

119   MOTU (meta-barcoding operational taxonomic units) estimate for those samples. Two,

120   phenotypic diversity [30,31] was assessed using the parameters returned by the flow

121   cytometre.

122

123   **Statistical analysis**

124   All data were analysed in the R programming environment (version 3.5.3.). To analyse the

125   shape of the growth curves, non-linear curve fitting of a baranyi growth model [34] was

126   carried out using the 'nlsLM' function in the R package, 'minpack.lm'(version 1.2-1). For

127   multi-model selection, we computed small sample-size corrected AIC scores (AICc) and then

128   compared the models by calculating delta AICc values and AICc weights using the "MuMIn"

129   package (version 1.42-1).

130

131   **Results:**

132   <u>Proof of concept</u>

133   MOTU (meta-barcoding operational taxonomic units) analyses revealed that biodiversity (as

134   species richness) was slightly higher for samples from the Kiel Bight than from the

135   Bornholm Basin sampling region (see Figure 1C and Figure S1), and roughly in line with

136   previous studies on Southern Baltic Sea phytoplankton communities [35]. Further, while

137   diversity was not reduced to a single species in the most dilute samples, MOTU data

138   confirmed that i) the most dilute samples were on average 10^5 times less species-rich than the

139   least dilute samples, ii) MOTU diversity scaled with phenotypic diversity (Figure S1) and

140   finally, that diversity once established by dilution, did not change significantly throughout the

141   time of the growth curve (Figure S2)

142

143   <u>Assay temperature and biogeography explain differences in functional redundancy</u>

144   We consider a result to be in line with high functional redundancy, when a function - such as

145   biomass production or net photosynthesis - does not change significantly across levels of

146   species richness. This results in slopes across dilution steps (i.e. species richness) that are

147   equal or close to zero. When a function declines with species richness, we assume low

148   functional redundancy. In these cases, the slope of trait value as a function of species richness

149   is *positive*. We report the steepness of these slopes across three assay temperatures in Figure

150   2 (Table S2 for slopes, and Tables S3 to S5 for model selection and output).

151

152   Across dilutions, temperature had a significant impact on biomass (Figure S3, likelihood ratio

153   test comparing models with and without 'temperature': Δ d.f. = 4, $\chi 2$ = 382.71, P < 0.0001,

154   Table S3). When communities lost rare species, biomass production did not change

155   significantly in the samples from the Kiel Bight (Figure 2A). Biomass production in samples

156   from the Bornholm Bight samples rapidly decreased when rare species were lost, resulting in

157   positive slopes (Figure S3, Figure 2A, likelihood ratio test comparing models with and

158   without 'region': Δ d.f. =2, $\chi 2$ = 185.23, P < 0.0001, Table S3).

159

160   Changes in biomass were driven by a change in cell number and a change in cell volume

161   across dilution steps, with a trend for smaller cells at higher species richness (Figure 2B, C,

162   Figure S4, S5, Table S2, S4). Cell volume decreased with temperature (likelihood ratio test

163   comparing models with and without 'temperature': Δd.f. = 2, $\chi 2$ =382.70, P < 0.0001, Figure

164   2C, Table S4). While cells in samples from the cooler, more stable, Bornholm Basin were on

165   average less reactive to temperature in terms of cell size, the effect of losing rare species was

166   stronger here than in samples from the Kiel Bight and cell size rapidly increased as species

167   richness decreased (likelihood ratio test comparing models with and without 'region: Δd.f. =

168   2, $\chi2 = 223.68$, $P < 0.0001$, Figure 2 C, Table S4)

169

170   Net Photosynthesis rates (NP) per cell followed a similar trend to biomass (Figure 2D, Figure

171   S6, Table S5 for model selection and output): assay temperature altered community NP

172   depending on dilution and sampling origin. Samples from the Kiel region were overall more

173   photosynthetically active than those from the Bornholm region (likelihood ratio test

174   comparing models with and without 'region': Δ d.f. $= 3$, $\chi2 = 21.63$, $P < 0.0001$, Figure 2D,

175   Figure S6, Table S5), especially at the warmer temperatures (likelihood ratio test comparing

176   models with and without 'temperature': Δ d.f. $= 1$, $\chi2 = 85.47$, $P < 0.0001$, Figure 2D Figure

177   S6, Table S5). NP in samples from the Kiel region showed no clear trend with dilution. In

178   samples from the Bornholm region, on the other hand, responses of NP to temperature were

179   overall less pronounced, but were strongly influenced by species richness, with the full

180   community samples photosynthesising nearly 1.5 times (per cell) as much as the samples

181   with the lowest species richness.

182
183   **Discussion**
184   Our investigations of the link between species richness and traits relevant for ecosystem

185   services showed that the steepness of the biodiversity-function slope hinged on the

186   communities' evolutionary histories as well as on short-term (ca 20 generations) changes in

187   temperature and fit well within the theoretical and observational general framework of

188   biodiversity/ecosystem function studies [2-5]. The effect of temperature modulating the

189   strength of the diversity/function relationship was the most pronounced for samples originating

190   from a cooler, less variable region, in line with theory predicting that regions that are more

191   variable should contain a greater number of taxa with more variable tolerance thresholds [36].

192

193   Overall, our findings are also in accordance with the literature on experimentally assembled

194   communities in microcosms, where the researchers found that a decline in productivity was

195   more pronounced at rising temperatures in phytoplankton and bacteria ([10] and [9]

196   respectively). We make the case that this pattern of declining productivity due to species loss

197   being enhanced at higher temperatures may be conserved across environments as diverse as

198   laboratory conditions and natural community samples. This may also mean that results

199   obtained from assembling artificial communities reflect results found in natural assemblages

200   well in direction, and possibly in magnitudes of responses. We specifically find that as species

201   are lost from samples with a history of comparatively cooler average temperatures and highly

202   predictable seasonal variation, the community rapidly shows a decrease in net photosynthesis

203   rates, biomass production, and – unlike in experimental assemblages [10] - an increase in cell

204   size. Changes in the biodiversity–ecosystem function relationship were thus strongly linked to

205   size-dependent turnover in community composition, but it is unclear whether this is a cause or

206   a consequence of the other observed patterns. We can only speculate about the underlying

207   mechanisms. While it is possible that competition for resources is stronger in a mixed

208   community, and that this pressure is relieved once most species are lost from the system, our

209   samples were kept in full media, and the pattern was obvious during exponential phase already

210   (Figure S7). It is thus unlikely that competition for nutrients, light, or space, was the main

211   factor here. Neither can the pattern be explained by the larger cells' being more common in the

212   original samples (which do have slightly higher variation in cell size than very dilute samples)

213   and therefore more likely to remain present after dilution. The pattern may be driven by

214   interactions beyond competition, e.g. types of facilitation [37], or a more general trend for trait

215   variability and biodiversity being intertwined [38]. It remains to be seen to which degree the

216   patterns we observed here are also driven by interactions with their associated bacteria. The

217   latter may have different nutrient requirements that are not met in the same way by our culture

218   media, which may in turn affect how they interact with and shape the phenotypes of the

219   phytoplankton species.

220

221   Irrespective of the reasons underlying the shift in cell size we observed here, the contribution

222   of the very small pico-phytoplankton cells to total phytoplankton biomass in the ocean has

223   been shown to increase with temperature [39] and changes to size distribution in scenarios

224   where warming and loss of biodiversity interact may have unpredictable impacts on the

225   function of phytoplankton ecosystems [40]

226

227   While biodiversity manipulation by dilution has limitations (e.g. diversity and species identity

228   can never be fully disentangled, dilution introduces quasi-random differences in beta diversity),

229   these apparent disadvantages have potential important ecological implications as they allow us

230   to specifically investigate the importance of rare taxa, rather than random species loss.

231

232   The Baltic Sea is generally low in species due to its characteristic brackish waters. To rule out

233   that our results are typical for regions where biodiversity (as richness) is low to begin with, it

234   would be necessary to carry out comparable studies across systems that vary in their initial

235   species compositions. Together, such data will further improve our understanding of the

236   relationship between diversity and ecosystem function at the foundation of warming aquatic

237   ecosystems.
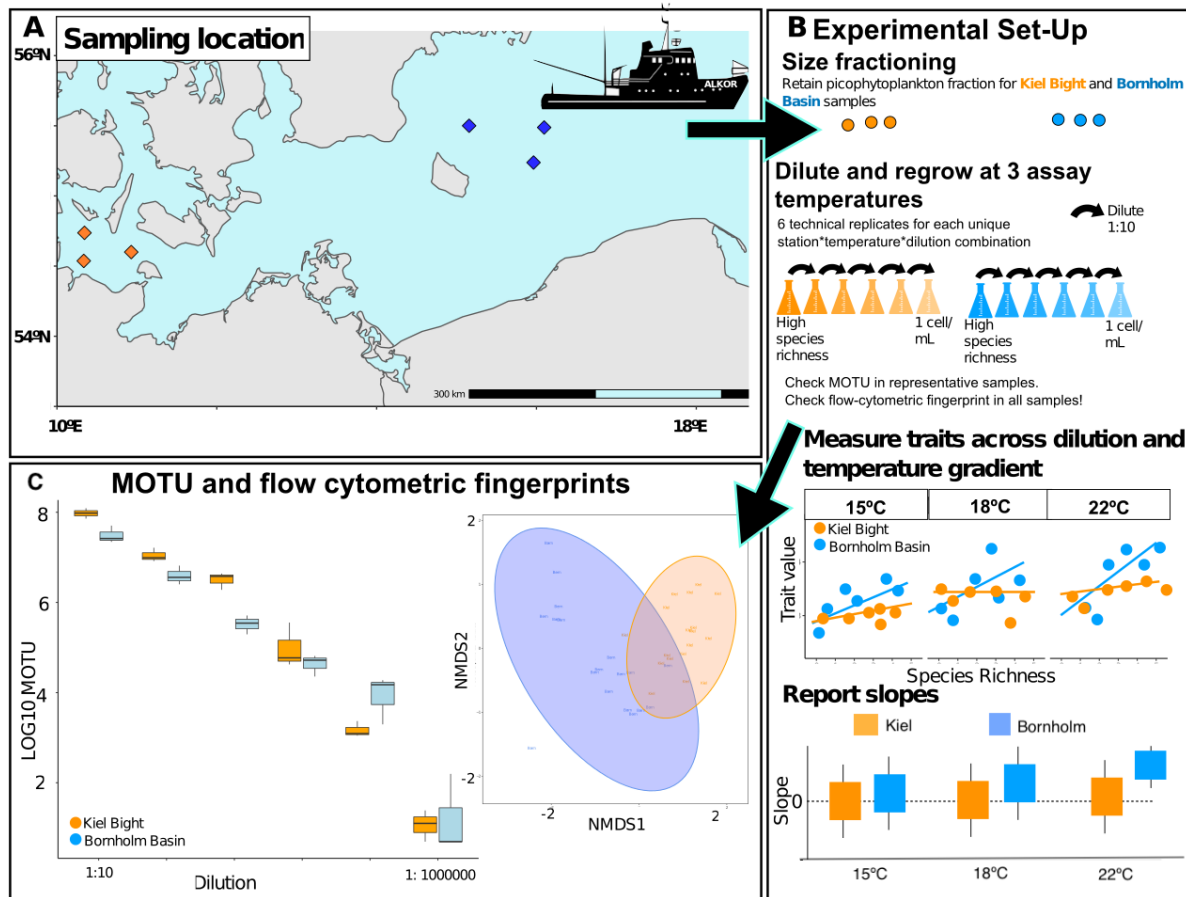
Figure 1: Overview of sampling locations, experimental set-up, and assessment of species richness via meta-barcoding and flow cytometry. A) sampling locations: We took samples in two biogeographically distinct regions of the Southern Baltic Sea: the Kiel Bight (KB, orange squares), and the Bornholm Basin (BB, blue squares) (Table S1). B) Set up and data-processing: The pico-phytoplankton fraction was obtained through size fractioning on board. Upon returning to the Institute for Marine Ecosystem and Fishery Science Hamburg (IMF), we established six technical replicates per community for each dilution across the three assay temperatures (15°C, 18°C, and 22°C). We report the slopes of three traits across the dilution steps for each region*assay temperature combination. C) Proof-of-concept via meta-barcoding and flow cytometry: To test our experimental design, we obtained MOTUs (Meta-barcoding Operational Taxonomic Units) and flow cytometric fingerprints (based on size and photopigment composition). While there were some regional differences in initial MOTU composition, those were overall not significant. (Figures S1 and S2).
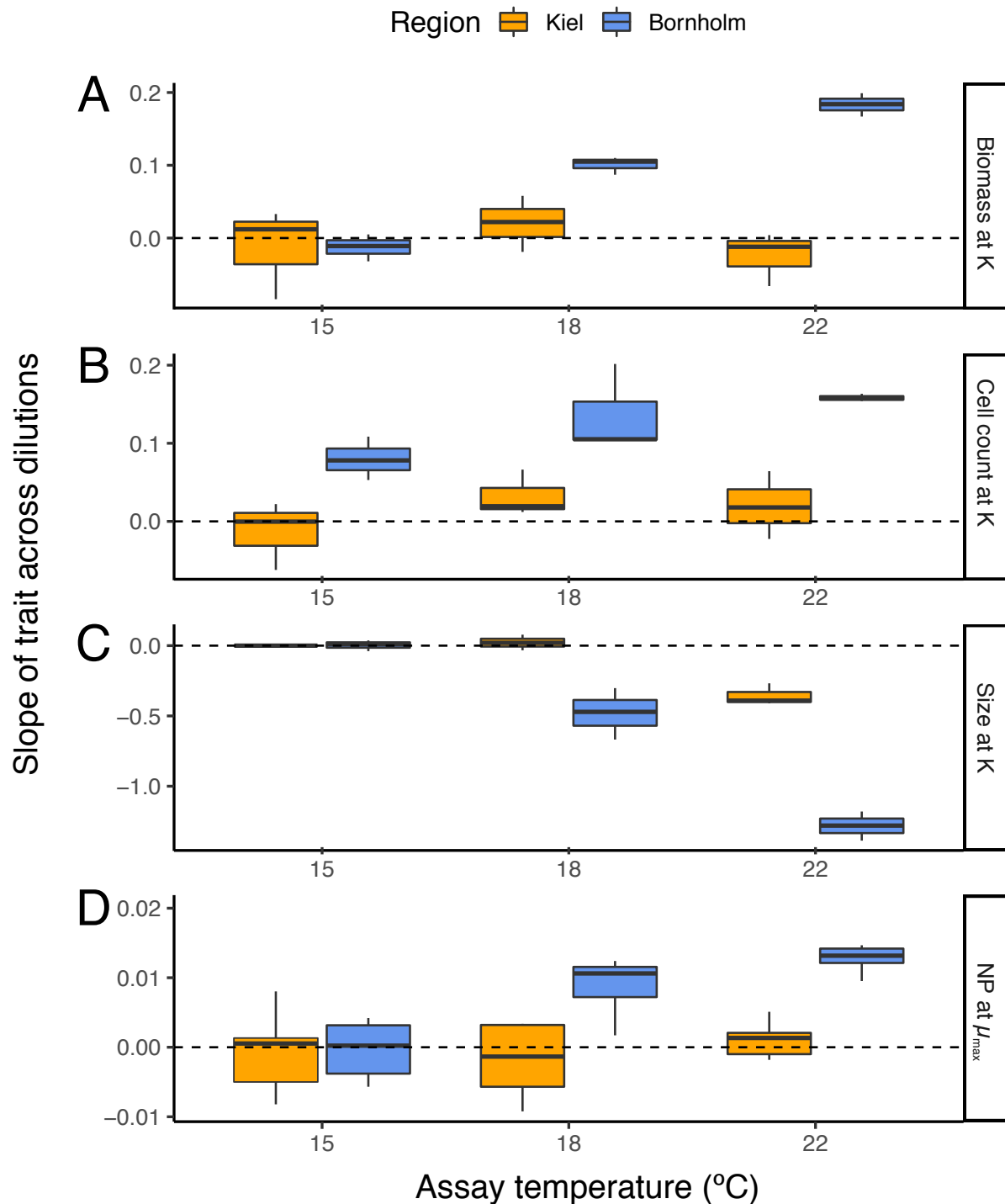
254
255 **Figure 2: Steepness of slopes for traits across dilution gradients** (see Figures S3 to S6 and
256 Table S2 for full slopes). The dashed line indicates a slope of 0, indicating high functional
257 redundancy, i.e. the trait does not change significantly as rare species are lost. A positive
258 slope indicates low functional redundancy, i.e. function decreases as species are lost. A
259 negative slope also indicates that function changes with species richness, and specifically
260 shows that a trait value decreases as species richness increases. **A**: Biomass produced at
261 carrying capacity is stable across dilution steps and temperatures for samples from the Kiel
262 Bight (high functional redundancy), however, there is low functional redundancy in samples
263 from the Bornholm Basin, especially under warming. **B:** Cell count (mL^{-1}) at carrying
264 capacity. Cell count followed the same pattern as overall biomass. **C:** Cell size at carrying

265   capacity. Average cell diameters were independent from dilution at 15°C for samples from
266   either region, but cells became smaller faster with temperature in the full communities as
267   compared to low species richness samples. This effect was more pronounced for samples
268   from the Bornholm Basin. **D**: Net Photosynthesis (NP) across dilution steps during
269   exponential growth showed similar patterns as the biomass response. Orange for Kiel Bight
270   samples, blue for Bornholm Basin samples. The boxplots are displayed as is standard, with
271   the girdle band indicating the median, and the whiskers extending to the 25th and 75th
272   percentile. n=6 for each unique combination. This plot only displays significant parameters,
273   i.e. samples from different seasons have been pooled.

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287   **References**

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422