

1 **Temperature is a poor proxy for synergistic climate forcing of plankton evolution**

2 Anieke Brombacher^{1*}, Paul A. Wilson¹, Ian Bailey², Thomas H.G. Ezard^{1,3}

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4 ¹Ocean & Earth Science, National Oceanography Centre Southampton, University of Southampton,
5 Waterfront Campus, European Way, Southampton SO14 3ZH, UK

6 ²Camborne School of Mines and Environmental Sustainability Institute, University of Exeter,
7 Penryn Campus, Cornwall TR10 9FE, UK

8 ³Biological Sciences, University of Southampton, Life Sciences Building 85, Highfield Campus,
9 Southampton SO17 1BJ, UK

10 *Corresponding author. Email: j.brombacher@noc.soton.ac.uk, phone nr: +44 7766 235205

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12

13 **Abstract**

14 Changes in biodiversity at all levels from molecules to ecosystems are often linked to climate
15 change, which is widely represented univariately by temperature. A global environmental driving
16 mechanism of biodiversity dynamics is thus implied by the strong correlation between
17 temperature proxies and diversity patterns in a wide variety of fauna and flora. Yet climate
18 consists of many interacting variables. Species likely respond to the entire climate system as
19 opposed to its individual facets. Here, we examine ecological and morphological traits of 12,629
20 individuals of two species of planktonic foraminifera with similar ecologies but contrasting
21 evolutionary outcomes. Our results show that morphological and ecological changes are
22 correlated to the interactions between multiple environmental factors. Models including
23 interactions between climate variables explain at least twice as much variation in size, shape and
24 abundance changes as models assuming that climate parameters operate independently. No
25 dominant climatic driver can be identified: temperature alone explains remarkably little variation
26 through our highly resolved temporal sequences, implying that a multivariate approach is
27 required to understand evolutionary response to abiotic forcing. Our results caution against the

28 use of a 'silver bullet' environmental parameter to represent global climate while studying
29 evolutionary responses to abiotic change, and show that more comprehensive reconstruction of
30 paleobiological dynamics requires multiple biotic and abiotic dimensions.

31

32 **1 Introduction**

33 Changes in biodiversity are often linked to climate change, usually temperature. Phanerozoic
34 species richness covaries with global temperature [1, 2]; Cenozoic diversity patterns of mammals
35 [3, 4], plants [5, 6], insects [6], plankton [7, 8] and benthic microfauna [9, 10] correlate with the
36 high-latitude climate signal recorded in the $\delta^{18}\text{O}$ composition of benthic foraminifera [11]. These
37 results imply a dominant mechanism shaping biodiversity dynamics through time. Yet climate
38 consists of many interacting variables, and species likely respond to the entire climate system as
39 opposed to separate variables: Harnik et al. [12] argued that simultaneous changes in multiple
40 environmental parameters drove most Phanerozoic extinction events, while Garcia et al. [13]
41 show increased threats on modern biodiversity become apparent when incorporating multiple
42 dimensions of climate change. However, the extent to which the impact of abiotic forcing on
43 within-species evolutionary change is underestimated when only single environmental factors
44 are assessed remains largely unknown. Evidence exists for both synergistic (combined effects of
45 multiple drivers are greater than the sum of individual drivers) and antagonistic (combined
46 effects of multiple drivers are smaller than the sum of individual drivers) processes in modern
47 ecosystems [14-16], but no empirical data exist for microevolutionary processes in deep time.

48

49 To accurately quantify the link between long-term (>10,000 years) microevolution and climate
50 change, high-resolution fossil records of multivariate evolutionary change need to be allied to
51 multivariate reconstructions of local environmental conditions. Such data are rarely available.
52 One of the few media on which multivariate evolutionary and environmental change can be
53 determined at high temporal resolution is the marine fossil record of planktonic foraminifera.
54 The excellent preservation of this group in open ocean sediments permits direct comparison of

55 morphological and ecological change to high-resolution records of climate and evolution
56 reconstructed from the same marine cores. Several studies have shown responses of
57 foraminiferal morphology to sea surface temperature [17-20], but many have also reported
58 relationships with productivity [21] and ocean stratification [17, 22]. However, none of these
59 studies analysed the ecological and evolutionary impacts due to the interplay of multiple climate
60 drivers.

61

62 Here we study species' response to multivariate climate change during the last great climate
63 transition in Earth's history: the late Pliocene to earliest Pleistocene intensification of Northern
64 Hemisphere glaciation (3.6-2.4 million years ago [Ma]) [23]. This interval was characterized by
65 major reorganizations of the global climate system: global atmospheric CO₂ concentrations [24]
66 dropped below the ~280 μ atm threshold for extensive Northern Hemisphere glaciation [25]
67 between 2.9-2.7 Ma (Figure 1c). By 2.7 Ma, continental ice-sheets had expanded significantly on
68 Greenland, Scandinavia and North America as evidenced by the onset of widespread ice-rafted
69 debris deposition in high northern latitude oceans [26, 27] and an increase in the amplitude of
70 glacial-interglacial cycles as recorded in benthic foraminifera $\delta^{18}\text{O}$ (to >0.5‰) from Marine
71 Isotope Stage (MIS) G6 (2.7 Ma) onwards (Figure 1a,b). In the North Atlantic Ocean this transition
72 to deeper glacials was associated with (i) incursions of southern-sourced deep waters [28], (ii) a
73 major intensification of dust flux from North America carried on the westerly winds [29, 30], and
74 (iii) increases in glacial primary productivity [30, 31] (Figure 1d,e). Together, these synergistic
75 environmental changes likely had a major impact on life in the marine realm [32]. All parameters
76 would have directly influenced individual foraminifera during their lifetime: species prefer
77 specific temperature ranges [33, 34] and will respond to temperature changes in their
78 environment [19, 20] as well as productivity regimes [35], while ocean pH influences calcification
79 potential [35]. To quantify the combined effects of changes in temperature, primary productivity,
80 dust input and atmospheric CO₂ on evolution during the intensification of Northern Hemisphere
81 glaciation, we employ multivariate statistical techniques to compare ecological (abundance,

82 Figure 1g) and morphological (size and shape, Figure 1h,i) dynamics across 12,629 specimens of
83 the ecologically similar planktonic foraminifera species *Globoconella puncticulata* and
84 *Truncorotalia crassaformis* (Figure S1). *Truncorotalia crassaformis* survived the intensification of
85 Northern Hemisphere glaciation and is still alive today, whereas *G. puncticulata* became extinct
86 shortly after 2.41 Ma (during MIS 96 [36]). These two foraminifer species provide an opportunity
87 to study species' responses to multivariate climate change under contrasting evolutionary
88 outcomes.

89

90 **2 Methods**

91 **2.1 Study species**

92 *Truncorotalia crassaformis* and *Globoconella puncticulata* (Figure S1) are two ecologically similar
93 species characterised by low trochospiral shells with flattened spiral sides, inflated umbilical
94 sides and umbilical-extraumbilical apertures [37]. Both inhabit thermocline to subthermocline
95 waters at middle and low latitudes [37, 38]. *Truncorotalia crassaformis* originated around 5.7 Ma
96 and survives to the present day. *Globoconella puncticulata* first appeared around 4.6 Ma and
97 became extinct at 2.41 Ma [36], shortly after the onset of significant Northern Hemisphere
98 glaciation at 2.72 Ma [27]. Our 500,000-year study interval includes the onset of wide-spread
99 Northern Hemisphere glaciation (MIS G6, 2.72 Ma, [27]), the first three major Northern
100 Hemisphere glaciations MIS 100, 98 and 96 [39], and ends with the extinction of *G. puncticulata*
101 [36]. Preservation of planktonic foraminifera is good throughout the study interval [40] implying
102 little dissolution effects on traits. We study three traits: mean shell area and mean aspect ratio
103 per time slice (data from [41]), which have been shown to be repeatable proxies for shell size and
104 shape [42], and abundance (this study) (Figure 1g-i). Schmidt et al. [43] show that maximum size
105 and abundance generally occur at the same temperature for modern planktonic foraminifera
106 species, implying that the combination of abundance and size are indicators of ecological optima
107 [43, 44]. Shell shape controls the area: volume ratio which influences respiratory processes
108 according to first principles of cell physiology.

109

110 2.2 Study site

111 IODP Site U1313 is located in the mid latitude North Atlantic Ocean at the base of the upper
112 western flank of the Mid-Atlantic Ridge at a water depth of 3426 m (41 °N, 32.5 °W) on the
113 northern edge of the North Atlantic subtropical gyre (Figure S2). The sediments deposited at Site
114 U1313 accumulated at consistently high rates (~5 cm/kyr) for the past 5 Myr [39, 40], and yield
115 a demonstrably continuous record of sedimentation through the intensification of Northern
116 Hemisphere glaciation [45] and exceptionally well-preserved microfossil carbonate [29].

117

118 We used 75 sediment samples from Site U1313 (every 30 cm, i.e. ~5-kyr-resolution) dated by
119 Bolton et al. [45] by matching an orbital-resolution benthic foraminiferal oxygen isotope ($\delta^{18}\text{O}$)
120 record to the global oxygen isotope stack [39]. The samples were dry-sieved over a >150 μm mesh
121 sieve and divided into equal fractions using a microsplitter until a single fraction contained 70-
122 150 specimens of *T. crassaformis* or *G. puncticulata*. The smallest analysed individual of *T.*
123 *crassaformis* is 30% larger than the smallest particle that could be captured by the sieve, so it is
124 unlikely we missed any specimens of this species by our choice of size fraction. For *G. puncticulata*
125 the smallest possible particle to be captured by the sieve is smaller than the species' mean shell
126 size minus 2 sigma, meaning >97.5% of all specimens would be captured by the current size
127 fraction, implying that the used size fraction has little effect on the data. To avoid size bias all
128 individuals from a single fraction were analysed, resulting in a total of 12,633 individuals (6058
129 specimens of *T. crassaformis* and 6575 of *G. puncticulata*) over the studied interval. The total
130 number of specimens in the sample was estimated by multiplying the number of individuals
131 found in the fraction by the total number of fractions into which the sample was split. Abundance
132 (represented as accumulation rates) was calculated as the number of individuals divided by the
133 weight of the sediment fraction larger than >150 μm^2 , divided by the total time in the sample as
134 determined by Bolton et al. [45]. Morphological trait data are available in the Dryad database as
135 part of [41]. Abundance data are deposited in the Figshare repository at

136 <https://figshare.com/s/9db6657150242fb8a593> and will be made publicly available upon
137 manuscript acceptance.

138

139 **2.3 Existing environmental reconstructions**

140 When comparing biotic to abiotic processes, global climate is often represented by oxygen isotope
141 records generated from foraminiferal calcite. However, these records form a composite of sea
142 water temperature, salinity and global ice volume, and mainly represent high-latitude climate.
143 Therefore, to directly compare species' responses to their immediate environment, local climatic
144 reconstructions are required. Several published orbitally resolved environmental reconstructions
145 are available for Site U1313, including n-alkane accumulation rates representing mixed-layer
146 productivity [46], terrestrial plant leaf wax fluxes linked to eolian input of North American dust
147 [30] and a mean annual sea surface temperature record based on the saturation index of C₃₇
148 alkenones (U^k₃₇) [30]. Although our study species inhabit thermocline waters, a comparison of
149 foraminifera test Mg/Ca ratio-derived sea surface and thermocline temperatures over the interval
150 ~2.4 – 2.6 Ma (Bolton et al., pers. Comm.) showed similar morphological response between our
151 study species, which agrees with findings from a study by Schmidt et al. [47] showing similar
152 response to temperature in species living at different depth habitats. Two plant wax records are
153 available for Site U1313, one based on n-alkanes and the other on C₂₆-alkan-1-ol chains. The two
154 records are highly correlated [30] and argued to be from a common North American origin [30].
155 As both are therefore likely to experience the same absolute level of noise, we chose to use the n-
156 alkanes record because its values are higher by a factor ~1.5 as compared to the C₂₆-alkan-1-ol-
157 based record, providing the highest signal: noise ratio. At present, the North Atlantic Subtropical
158 Gyre is nutrient limited with nitrogen fixation correlated to dissolved iron [48] and the strong
159 correlation between aeolian input and productivity in the late Pliocene (see Figure 1d,e) implies
160 that this was to an extent also true for our study interval. Biotic responses were compared to the
161 site-specific reconstructions of sea surface temperature, productivity and dust input [30, 46], and
162 a global reconstruction of atmospheric CO₂ concentration [24] to represent multiple dimensions

163 of environmental conditions experienced by the study species (Figure 1c-f). Although
164 reconstructed from an equatorial site, the atmospheric CO₂ reconstruction is likely to reflect
165 changes in pH at IODP Site U1313 induced by atmospheric CO₂ as well given the short mixing time
166 of CO₂ between the sea surface and the atmosphere [24]. Additionally, Site U1313 likely
167 experienced little oceanographic change during the intensification of Northern Hemisphere
168 glaciation [49] implying a constant local CO₂ balance. Aeolian dust is used here to indicate nutrient
169 levels, as dust provides an additional nutrient source to the oligotrophic and iron-limited
170 subtropical gyre [48], and ocean pH influences calcification potential, influencing selection for
171 larger shell size and thickness with decreasing pH [35]. Although these parameters only represent
172 a subset of all environmental change, comparing species' responses to these parameters and their
173 combinations will shed new light on multivariate drivers of evolutionary change.

174

175 **2.4 Analysis**

176 Because the environmental reconstructions of Site U1313 and the foraminifera trait data were
177 generated using different sample sets, the climate data point ages are offset relative to our
178 foraminifera samples. Generalised Additive Models (GAMs) were employed to interpolate the
179 climate parameters to the foraminiferal sample ages. The individual climate records were
180 smoothed using a GAM, and the value at the age of the foraminifera samples was estimated using
181 the non-parametric curve (Figure 2). To enable comparisons of responses among traits we
182 studied the morphological trait means and single abundance values per time slice. To compare
183 trait changes to climate change, first differences of all biotic and environmental records were
184 calculated to remove temporal autocorrelation in the residuals (supplementary figures S3 and
185 S4). Using Linear Models the first difference of the trait records were then compared to those of
186 the environmental parameters to calculate the total variance explained in the biotic parameters
187 to change in the environmental parameters and their interactions. Trait variance explained by
188 individual parameters was calculated as the variance explained (R²) by the full model (up to and
189 including all two-way interactions), minus the variance explained by the model with each

190 parameter removed [50]. Another Linear Model with only univariate effects was compared to our
191 full model to quantify the synergistic effects of interactions among climate variables on
192 morphological and ecological change. We focus on the R^2 value due to its tractability, and the
193 possibility to study effect sizes of all climate variables and their interactions. Δ Akaike Information
194 Criterion (AIC) scores of individual parameters and interactions are included in supplementary
195 figure S5.

196

197 **3 Results**

198 In all cases, most variation of that explained by models was through the combination of all studied
199 parameters and their interactions (7.1%, 17.3% and 17.3% for *G. puncticulata* size, shape and
200 abundance, and 10.9%, 18.3% and 26.6% for *T. crassaformis* size, shape and abundance). No
201 single driver is found to dominate the variance explained in all studied traits (Figure 3). Variation
202 in size of *G. puncticulata* and size and shape of *T. crassaformis* are most strongly correlated to
203 temperature (5.5%, 8.2% and 7.3% for *G. puncticulata* size, and *T. crassaformis* size and shape
204 respectively), whereas productivity is most strongly correlated to shape in *G. puncticulata* (13.9%
205 variance explained) and abundance of *T. crassaformis* (20.5% variance explained). Abundance of
206 *G. puncticulata* is best explained by aeolian input (14.8% variance explained). However, in all
207 three cases little variance is explained by these parameters alone.

208

209 The model including all two-way interactions provides a significantly better fit to the data than
210 the additive model without the interactions for shape in *G. puncticulata* (ANOVA, $F_{6,69} > 2.1$, $p <$
211 0.05), and abundance in *T. crassaformis* (ANOVA, $F_{6,69} > 2.4$, $p < 0.05$). In both species, response
212 of abundance is most strongly correlated to the environmental parameters (Wilcoxon signed-
213 rank test, $p < 0.01$ and $p < 0.05$ for *G. puncticulata* and *T. crassaformis* respectively) but no
214 difference was detected between the responses of size and shape (Wilcoxon signed rank test, $p =$
215 0.79 and $p = 0.74$ for *G. puncticulata* and *T. crassaformis* respectively). Response of size is stronger
216 in *G. puncticulata* than *T. crassaformis* (Wilcoxon signed-rank test, $p < 0.01$), but the strength of

217 responses is comparable between species for shape and abundance (Wilcoxon signed-rank test,
218 $p = 0.65$ for shape, $p = 0.69$ for abundance).

219

220 **4 Discussion**

221 Our results show that temperature is a poor proxy for synergistic climate forcing of the observed
222 biotic change. The amount of morphological and ecological variation explained is highest when
223 studied including interactions between multiple environmental parameters. These results imply
224 that species' response to climate change can be underestimated when only single variables are
225 taken to represent the complex multifaceted climate system: in our study the amount of biotic
226 variance explained by environmental change decreases by up to a factor ~ 2 if only single
227 variables are considered (Figure 3), and is likely to decrease further relative to multivariate
228 change with more drivers included in the analyses. Our findings are consistent with short-term
229 studies of modern populations that show increased mortality as a response to multiple
230 environmental stressors [14, 15, 51], as well as macroevolutionary research into the abiotic
231 drivers of mass extinctions [12, 13]. The strength of the correlation between environmental
232 parameters and traits varies – no single parameter best explains the variance in all records.
233 Therefore, our results caution against the use of a single “silver bullet” environmental parameter
234 to represent global climate while studying evolutionary response to abiotic change.

235

236 Our results generate an appropriately multi-faceted picture of abiotic forcing, and suggest
237 strongly that (sea surface) temperature alone is a poor proxy for environmental changes that
238 supposedly drive ecological and morphological changes through time. These results contrast with
239 the findings of spatial studies by Tittensor et al. [52], Rutherford et al. [53] and Fenton et al. [54],
240 who used multiple species of planktonic foraminifera to report the dominance of temperature in
241 shaping ecological processes across space. The comparison of these results implies that spatial
242 abiotic drivers [54] do not directly translate to those operating through time along single species'
243 branches, supporting hypotheses that spatial variation is not a suitable substitute for temporal

244 change and that data with a substantial temporal component are required to accurately
245 reconstruct biodiversity dynamics over long time scales [55, 56].

246

247 Neither species' responses are synergistic (total response > sum of response to individual
248 parameters) because response to the total model describes less trait variance than the sum of the
249 responses to single climate variables. These results are consistent with the findings of Darling et
250 al. [16], who reviewed 112 published mortality experiments and found only a third showed
251 synergistic responses to external drivers. In our case, the species' antagonistic responses (total
252 response < sum of response to individual parameters) to abiotic change could be explained by a
253 common driving mechanism underpinning the studied environmental variables. Late Pliocene
254 North Atlantic sea surface temperature, productivity, aeolian dust input and CO₂ are all correlated
255 and strongly linked to the intensification of Northern Hemisphere glaciation [24, 27-30, 46],
256 resulting in similar trends in each record (Figure 1c-f) that are expected to add little extra
257 variance explained in the biotic records. Depending on its ecological preferences, a species could
258 respond to parameters in opposite ways: a positive response to an increase in one variable and a
259 negative response to increase in another could lead to little net effect when both variables
260 increase, decreasing the variance explained by the total model. This further advocates the use of
261 multiple environmental parameters in the model as it allows exploration of synergistic or
262 antagonistic responses that would otherwise have remained unknown.

263

264 The unexplained variance in size, shape and abundance dynamics could be attributable to several
265 factors. Firstly, planktonic foraminifera have a life span of a few weeks [35]. Individuals living in
266 different seasons in the mid-latitude Atlantic Ocean experience temperature differences of up to
267 6-7 degrees Celsius [57]. Such variability is comparable to mean annual Late Pliocene – Early
268 Pleistocene glacial-interglacial SST changes at our study site [46, 49] (Figure 1f) and plastic
269 responses to these seasonal differences could increase trait variance in our time-averaged
270 samples. Secondly, some of the observed trait variance could be caused by migration of

271 morphologically distinct populations. However, the position of major surface water currents
272 likely remained unchanged throughout our study interval [49], providing little opportunity for
273 migrations of populations from other areas. Third, abundance and shell shape responded more
274 strongly to the studied environmental variables than shell size, but in reality traits are often not
275 independent [58, 59]. Such covariation can constrain evolutionary responses to environmental
276 drivers [60]. Climatic upheaval can disrupt the covariation between traits [41], emphasising the
277 need for comprehensive understanding of abiotic catalysts for biotic change.

278

279 **5 Conclusion**

280 We show that morphological and ecological change through time correlate to multivariate
281 environmental change, particularly the interactions between distinct parts of global climate. No
282 single climate variable was identified that best explained morphological and ecological change in
283 all studied traits of both foraminifera species, implying that responses to environmental change
284 are likely to be severely underestimated when only single variables such as temperature are used
285 to represent global climate. Temperature was not even the most important single climate variable
286 explaining morphological or ecological variation. Responses also varied among morphological
287 and ecological traits, suggesting trait-specific sensitivities to environmental change that require
288 comprehensive comparative analyses to tease apart. Our results imply that use of local
289 temperature as a single variable to test for biotic response to climate change is limiting. Successful
290 reconstruction of eco-evolutionary dynamics in deep time therefore necessitates multivariate
291 explanatory and response variables.

292

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302

303 **Data accessibility**

304 Abundance data: Figshare <https://figshare.com/s/9db6657150242fb8a593>

305

306 **Competing interests**

307 We have no competing interests

308

309 **Authors' contributions**

310 AB participated in the design of the study, carried out the lab work, participated in the statistical
311 analysis and drafted the manuscript. IB participated in the design of the study and helped draft
312 the manuscript. PAW participated in the design of the study, coordinated the study and helped
313 draft the manuscript. THGE designed the study, participated in the statistical analysis of the data,
314 coordinated the study and helped draft the manuscript. All authors gave final approval for
315 publication.

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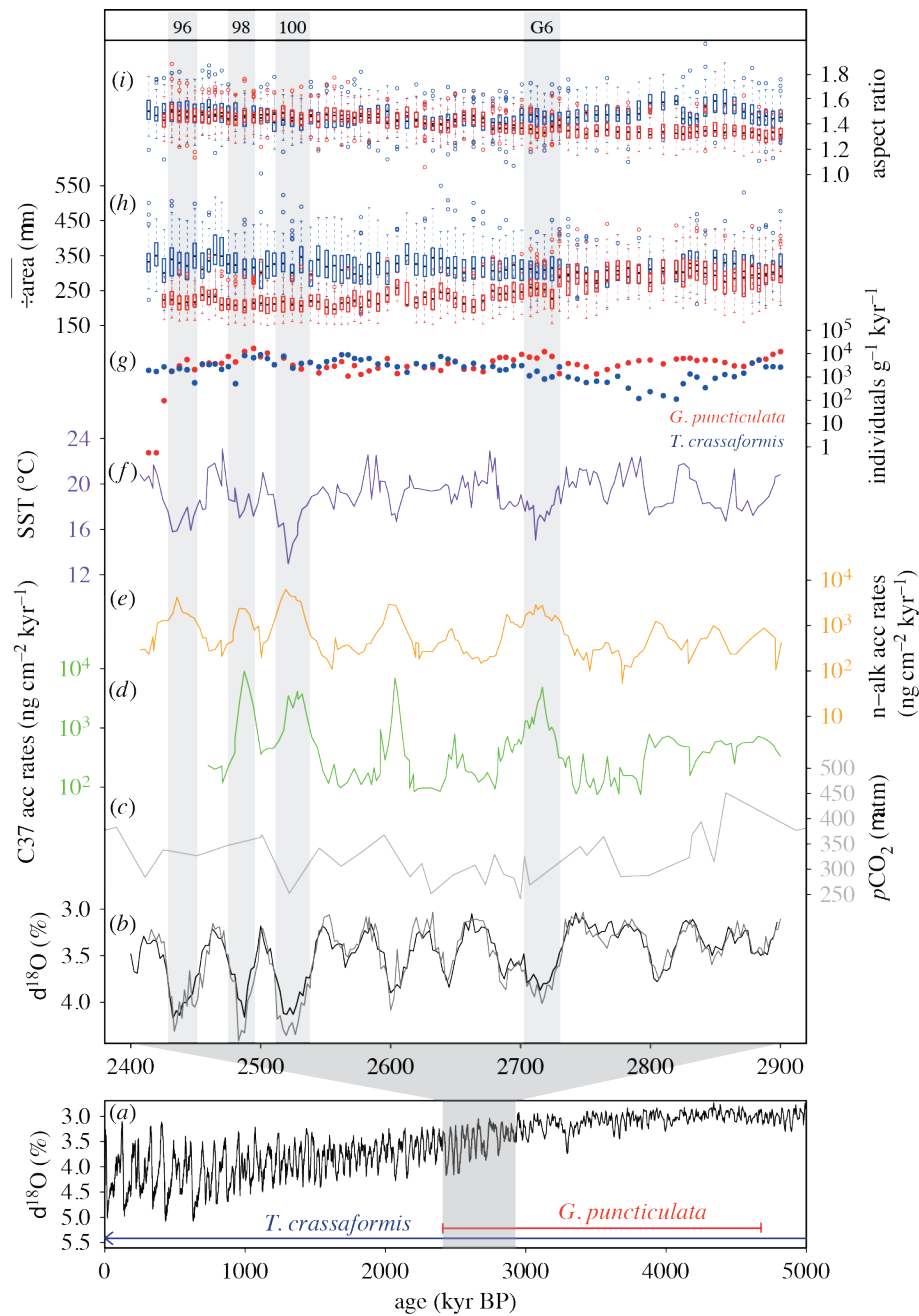
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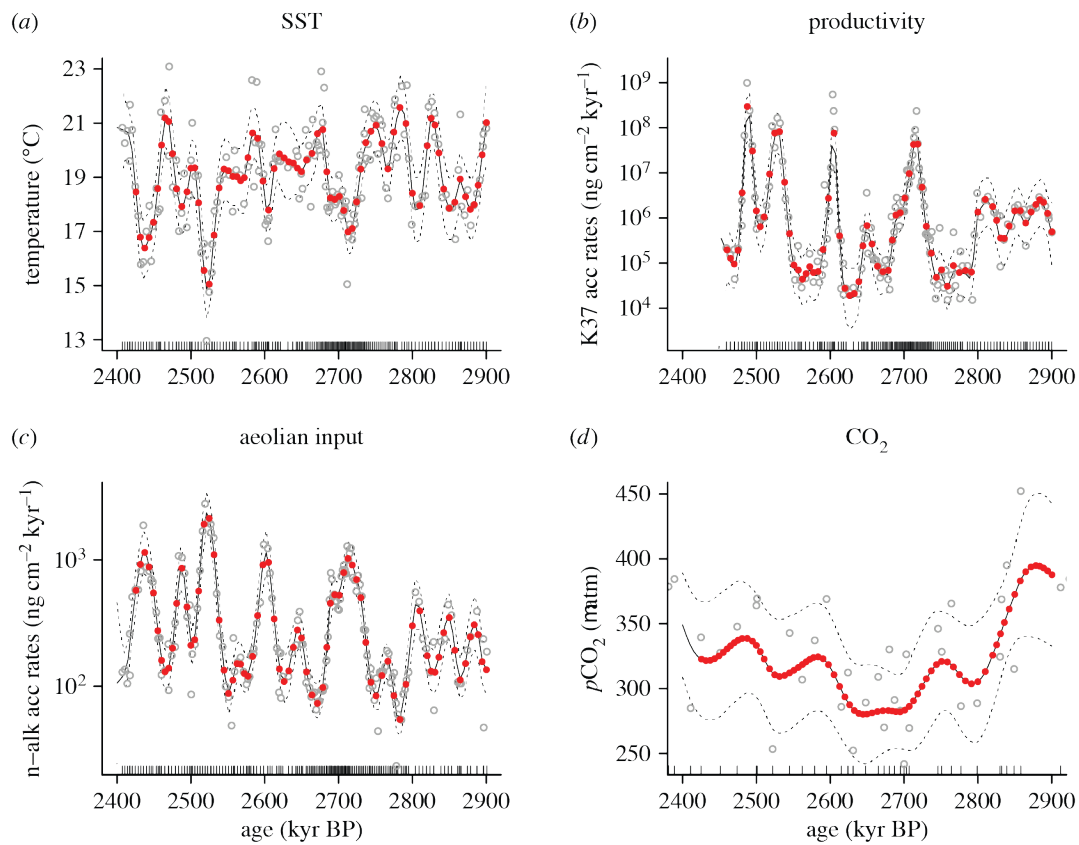
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480

481 Figure 1

482 Environmental reconstructions and morphology of two planktonic foraminifera species at IODP
 483 Site U1313: Oxygen isotopes from the Lisiecki et al. [39] benthic stack (a,b, black lines) and Site
 484 U1313 [45] (b, grey line), atmospheric CO_2 reconstructed at ODP Site 999 by Martínez-Botí et al.
 485 [24] (c), productivity (d), eolian input (e) and sea surface temperature (f) by Naafs et al. [30],
 486 abundance (g) of *Globoconella puncticulata* (red) and *Truncorotalia crassaformis* (blue) (this
 487 study), and size (h) and shape (i) of *G. puncticulata* and *T. crassaformis* [41]. Key glacial stages
 488 are indicated by grey bars.

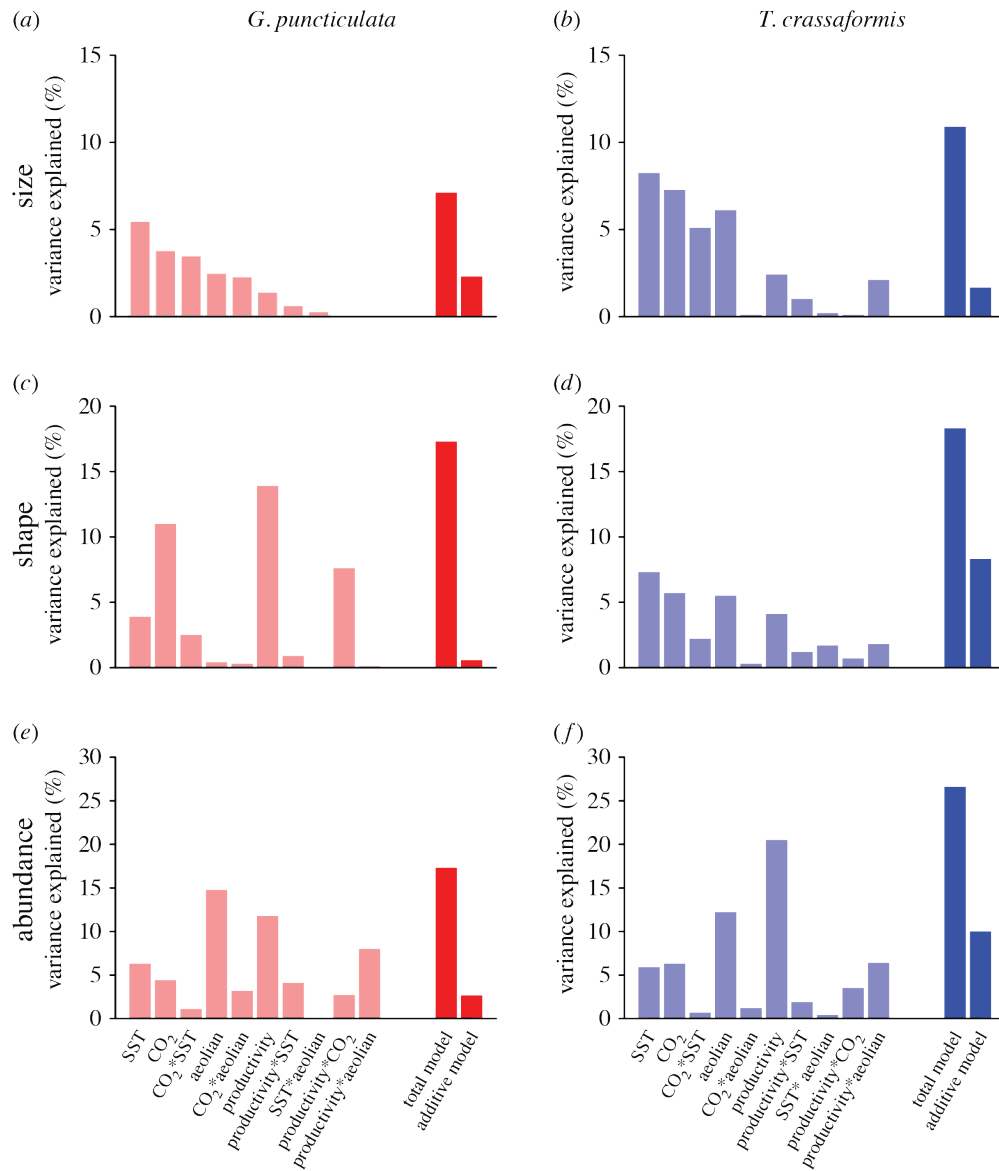


489

490 Figure 2

491 Generalised Additive Models (GAM) used to interpolate values of sea surface temperature (a),
 492 productivity (b), eolian dust input (c) and atmospheric CO₂ concentration (d) at the ages of the
 493 foraminifera samples from Site U1313 (internal tick marks on x-axis). Original data points are
 494 denoted by open circles, with solid and dashed lines representing the GAM and 95% confidence
 495 interval respectively. Estimated values are indicated by red circles.

496



497

498 Figure 3

499 Variance explained in size (a,b), shape (c,d) and abundance (e,f) of *Globoconella puncticulata* (red)

500 and *Truncorotalia crassaformis* (blue) from North Atlantic Site U1313 (41°N) by the

501 environmental parameters and their interactions.

502

503