Projected impacts of climate change and ocean acidification on the global biogeography of planktonic foraminifera

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1 **Abstract**

2 Planktonic foraminifera are a major contributor to the deep carbonate-flux and their microfossil

3 deposits form one of the richest databases for reconstructing paleoenvironments, particularly through

4 changes in their taxonomic and shell composition. Using an empirically-based planktonic foraminifer

5 model that incorporates three known major physiological drivers of their biogeography—temperature,

6 food and light—we investigate i) the global redistribution of planktonic foraminifera under

7 anthropogenic climate change, and ii) the alteration of the carbonate chemistry of foraminiferal habitat

8 with ocean acidification. The present-day and future (2090–2100) 3D distributions of foraminifera are

9 simulated using temperature, plankton biomass, and light from an Earth system model forced with

10 historical and a future (IPCC A2) high CO_2 emission scenario. Foraminiferal abundance and diversity

11 are projected to decrease in the tropics and subpolar regions and increase in the subtropics and

12 around the poles. Temperature is the dominant control on the future change in the biogeography of

13 foraminifera. Yet food availability acts to either reinforce or counteract the temperature driven

14 changes. In the tropics/subtropics the largely-temperature driven shift to depth is enhanced by the

15 increased concentration of phytoplankton at depth. In the higher latitudes the food-driven response

16 partly offsets the temperature-driven reduction both in the subsurface and across large geographical

17 regions. The large-scale rearrangements in foraminiferal abundance and the reduction of the

18 carbonate ion concentrations of the habitat range of planktonic foraminifers—from 10–30 μmol kg^{-1} in

19 their polar/subpolar habitats to 30–70 μmol kg^{-1} in their subtropical/tropical habitats— would be

20 expected to lead to changes in the marine carbonate flux. High-latitude species are most vulnerable

21 to anthropogenic change: their abundance and available habitat decrease and up to 10% of the

22 volume of their habitat drops below the calcite saturation horizon.

23

1. Introduction

25 Large-scale changes to the biogeography and shell chemistry of planktonic foraminifera have the

26 potential to alter the marine carbonate flux as planktonic foraminifera form shells of calcium carbonate

27 (tests). Through the sinking of their tests to the seafloor, planktonic foraminifera contribute as much

28 as 32–80% to the global flux of calcium carbonate (Schiebel, 2002), despite their relatively sparse

29 distribution throughout the ocean (Buitenhuis *et al.*, 2013). Thus, they represent one of the three

30 planktonic groups that dominate the oceanic carbonate flux alongside coccolithophores and

31 pteropods (Honjo, 1996). Indeed, much of the seafloor is covered by foraminiferal tests. This is partly

32 due to the efficient transport of foraminifera to the ocean floor since they are comparatively large

33 (mostly between 0.01 to 1 mm) and have rapid sinking speeds (Berger & Piper, 1972). Also, the tests

34 of foraminifera are relatively well preserved because they are composed of calcite: the less soluble of

35 the biogenic forms of calcium carbonate.

36 Under future scenarios of climate change, ocean acidification is projected to reduce the carbonate

37 production by planktonic calcifiers (Orr et al., 2005). As the ocean absorbs excess atmospheric CO_2,

38 the increase in dissolved CO_2 results in a reduction in pH (i.e. an increase in acidity) and a reduction

39 in the concentration of carbonate ions $[CO_3^{2-}]$. This decrease in carbonate concentration makes it

40 more difficult for calcifying organisms to form biogenic calcium carbonate. It also leads to a reduction

41 in the calcium carbonate saturation state (Ω_C) of the oceans (Feely et al., 2004), where

42 $\Omega_C = \dfrac{\left[\text{Ca}^{2+}\right]\left[\text{CO}_3^{2-}\right]}{K_{sp}^{CaCO_2}}$, $[Ca^{2+}]$ and $[CO_3^{2-}]$ are the calcium and carbonate ion concentrations and K_{sp}

43 is the stoichiometric solubility product of calcite ($CaCO_3$).

44 Present-day responses of planktonic foraminifera to anthropogenic change should provide a 'living

45 laboratory' for interpreting past responses to climatic change that have been recorded in the

46 sediments over geological timescales. Foraminifera are expected to be useful biological indicators of

47 anthropogenic climate change in the marine environment because:

48   •   foraminifera are established proxies of past climatic conditions (Kucera *et al.*, 2005) and, by

49   corollary, should 'record' future climate change,

50   •   the present-day global distribution of foraminifera is one of the most well known of all oceanic

51   taxa (Rutherford *et al.,* 1999), and can provide a useful baseline for measuring change,

52   •   there are no known specific predators of foraminifera (Hemleben *et al.,* 1989), so, changes in

53   the distributions of foraminifera are more likely to reflect climatic rather than ecological

54   changes,

55   •   the spatial distributions of pelagic organisms are expected to shift faster in response to

56   climate change than demersal species (Pereira *et al.*, 2010),

57   •   the growth rates and abundances of foraminifera are very responsive to changes in

58   temperature, particularly at the limit of their temperature range (Rutherford *et al.*, 1999),

59   •   historical changes in foraminiferal abundance have been shown to reflect anthropogenic

60   climate change (Field *et al.*, 2006), and

61   •   changes in the abundance and distribution of foraminifera are well preserved in ocean

62   sediments, and can be measured from plankton tows and sediment traps.

63 Temperature, food availability and light traits demarcate much of the foraminiferal distribution

64 throughout the global ocean (Hemleben *et al.*, 1989). Temperature exerts a first order control on the

65 distribution of foraminifera (Rutherford *et al.*, 1999). Each species has a unique optimum temperature

66 range with a fairly sharp drop in their growth rates at either extreme (Lombard *et al.*, 2009a; Figure

67 S1). Yet other factors have been shown to influence the distribution patterns of foraminifera (e.g.

68 Fairbanks *et al.*, 1982; Bijma *et al.*, 1990; Bijma *et al.*, 1992). Light also plays an important role in the

69 distribution of many foraminifera species, both directly through providing energy to the algal

70 symbionts hosted by some species of foraminifera (Spero & Lea, 1993), and indirectly by controlling

71 the distribution of the foraminiferal prey (Bijma *et al.*, 1992). There are some generalizations that can

72 be made about the broadscale biogeography of foraminifera based on light availability. Planktonic

73 foraminifera can be divided into to two groups based on whether or not their tests carry spines

74 (spinose) or not (non-spinose). Many of the spinose species host algal symbionts that can contribute

75 to the growth of the foraminifera. Species with algal symbionts are generally optimized for shallow,

76 high-light, low-nutrient environments, so dominate the abundance in the oligotrophic gyres. Some

77 symbiont-barren species, such as *G. bulloides* and *N. pachyderma*, are optimized for survival in

78 regions with high productivity. Prey availability has also been shown to have a significant impact on

79 the distribution of foraminifera (Ortiz *et al.*, 1995; Watkins *et al.*, 1996; Watkins *et al.*, 1998). The

80 spinose species have calcareous spines that assist in prey capture and tend to be carnivorous or

81 omnivorous, feeding on copepods and other zooplankton; while the nonspinose species tend to prefer

82 phytoplankton (Spindler *et al.*, 1984).

83 Given the sensitivity of planktonic foraminifera to environmental change and their contribution to the

84 global carbonate flux, it is timely to address how the planktonic foraminifera could respond to

85 anthropogenic perturbations of the oceanic environment. Changes in the characteristics of planktonic

86 foraminiferal assemblages preserved in microfossil-rich sediments, and knowledge of the

87 ecophysiological traits of foraminifera species, has helped to reconstruct past environmental

88 conditions to as far back as 120 million years ago. Here, we reverse the problem and project the

89 future change by the end of the century in both i) the 3D biogeography of planktonic foraminifera

90 based on their physiological sensitivities to environmental conditions (temperature, food and light),

91 and ii) the carbon chemistry of their habitat with ocean acidification.

92 2. Materials and methods

93   *2.1. Earth system model and simulations*

94 To simulate the present-day and future global ocean environments we used the Institut Pierre-Simon

95 Laplace Coupled Model 4 (IPSL-CM4) model. The IPSL model couples the Laboratoire de

96 Météorologie Dynamique atmospheric model (LMDZ-4), with a horizontal resolution of about 3×2.5°

97 and 19 vertical levels (Hourdin *et al.*, 2006) to the OPA-8 ocean model, with a horizontal resolution of

98 $2° \times 2° \cdot \cos\varphi$, 31 vertical levels and a surface ocean thickness of 10 m, and the LIM sea-ice model

99 (Madec *et al.*, 1998). The terrestrial biosphere is represented by the global vegetation model

100   ORCHIDEE (Krinner *et al.*, 2005) and the marine biogeochemical cycles by the PISCES model

101   (Aumont *et al.*, 2003).

102   PISCES simulates the cycling of carbon, oxygen, and the major nutrients determining phytoplankton

103   growth (PO_4^{3-}, NO_3^-, NH_4^+, Si, Fe). Phytoplankton growth is limited by the availability of external

104   nutrients, as well as temperature, and light. The model has two phytoplankton size classes (small and

105   large), representing nanophytoplankton and diatoms, as well as two zooplankton size classes (small

106   and large), representing microzooplankton and mesozooplankton. The C:N:P ratios are assumed

107   constant 122:16:1 (Anderson & Sarmiento, 1994), while the internal ratios of Fe:C, Chl:C, and Si:C of

108   phytoplankton are predicted by the model. For more details on PISCES see Aumont and Bopp (2006)

109   and Gehlen et al. (2006).

110   To produce the simulations used here, the IPSL model is forced with historical (1860–1999) CO_2

111   emissions (Marland and Andres, 2005) and the IPCC AR4 A2 high CO_2 emission future (2000–2100)

112   scenario (Nakicenovic et al. 2000). To calculate the input fields for the FORAMCLIM model (i.e. ocean

113   temperature, *T*; total phytoplankton concentration, *PHY*; photosynthetically active radiation, *PAR*; and

114   the carbonate ion concentration, CO_3^{2-}) a monthly climatology is calculated by averaging the drift-

115   corrected fields over two ten-year periods: present (2000–2009) and future (2090–2099). These IPSL

116   model simulations have been evaluated over the historical period (Schneider et al., 2008) and have

117   contributed to multimodel studies of the future change in marine primary productivity (Steinacher et

118   al., 2010) and the carbon cycle (Roy et al., 2011).

119   *2.2. Foraminifera model (FORAMCLIM)*

120   We use the FORAMCLIM model (Lombard *et al.*, 2011) to simulate the growth rates and the

121   abundances of eight common and widely-studied foraminiferal species. Five of the simulated species

122   are spinose (*Orbulina universa, Globigerinoides sacculifer, Globigerinoides ruber, Globigerinella*

123   *siphonifera, Globigerina bulloides*) and three species are nonspinose (*Neogloboquadrina dutertrei,*

124   *Neogloboquadrina incompta, Neogloboquadrina pachyderma*). The FORAMCLIM model incorporates

125   i) the response of each species of foraminifera to multiple environmental drivers (food, temperature

126   and light) and ii) the impact of these drivers on independent process (photosynthesis, nutrition and

6

127   respiration). Growth rates in the model are the result of the antagonism between food inputs (nutrition,

128   photosynthesis) and the physiological expenses of the organisms (respiration). For a full appreciation

129   of the model design, readers are encouraged to refer to the model description in Lombard *et al.*

130   (2011) and references therein.

131   The growth-rate relationships in FORAMCLIM were based on the observed physiological responses

132   of living specimens under controlled laboratory conditions (Lombard et al., 2009a; Lombard et al.,

133   2009b; Lombard *et al.*, 2011). In FORAMCLIM, the daily growth rate μ (d^{-1}) is calculated as $\ln(W_f/W_i)$,

134   where W_f and W_i are the final and initial weights of the foraminifera over a one day period. The

135   change in weight, ΔW, ($\mu gC\ d^{-1}$)—that is, the species-specific change in weight of a 250 μm individual

136   per day—is simulated based on three main physiological rates: nutrition (N), respiration (R) and

137   photosynthesis by the algal symbionts (P).

$$\Delta W(T,F,PAR) = N(T,F) + P(T,PAR) - R(T) \tag{1}$$

139   These physiological rates are a function of ocean temperature (T), light (PAR, photosynthetically

140   active radiation) and food concentration (F). Here, the total phytoplankton concentration (PHY) is

141   used as a proxy for F, according to Lombard *et al.* (2011). We use the 3D decadal-mean climatologies

142   of $T, F,$ and PAR for present and future time slices of the IPSL model simulations.

143   The relationships between growth rates and abundances were calibrated against abundances

144   observed in multinet plankton tows (Lombard *et al.*, 2011). Based on the strong relationship between

145   physiological rates and abundances observed in multinet plankton tows, an exponential relationship

146   between abundance ($Abund$, individuals per m^3) and μ was assumed (Lombard *et al.*, 2011), where

$$Abund = a\ \mu^b - a + 0.1 \tag{2}$$

148   Generally, the abundance, or standing stock in the water column, is given by the annual mean

149   $\sum_{t=1:12} \dfrac{Abund_i(t)}{12} dt$. In the cases where we estimate the maximum abundance that could potentially

150   reach the ocean sediments, the monthly-mean depth-integrated abundances are integrated over the

151 seasonal cycle $\sum_{t=1:12} Abund_i(t) dt$. The relative abundances, *Rabund*, for each species are

152 $$Rabund_i = \frac{Abund_i}{\sum_{i=1:8} Abund_i} \text{ x } 100\% .$$

153 All the physiological parameters are species-specific. The most relevant parameters to this study are

154 listed in Table 1. The contribution of photosynthetically-derived organic matter to the nutrition rate is

155 set by both $^{\%}p$, the fraction of the symbiont photosynthesis that is utilized in foraminiferal growth, and

156 s_{nb}, the number of algal symbionts per 250 μm individual (Table 1). Photosynthesis only contributes to

157 the growth rate in species that bear algal symbionts. The food-driven component of the foraminiferal

158 nutrition rate is largely dependent on the half-saturation constant for the Michaelis-Menten

159 relationship, k_n. Species with lower k_n, tend to be more adapted to oligotrophic waters, while species

160 with high k_n tend to require higher food concentrations for growth.

161   *2.3. Foraminiferal assemblage and calcite saturation data*

162 For model evaluation we use two independent data sets: i) the surface abundances from global

163 plankton tows (Bé & Tolderlund, 1971), and ii) the relative abundances from sediment top cores. The

164 observed relative abundances of foraminifera in sediment cores (Figure S2a) are compiled from the

165 MARGO database (Barrows & Juggins, 2005; Hayes *et al.*, 2005; Kucera *et al.*, 2004). Although the

166 key focus of the MARGO database is the reconstruction of sea surface temperatures, the relative

167 abundances are also available. We compiled all the available relative abundances in the MARGO

168 database from the top cores and recalculated the relative abundances based on only the eight

169 species used in this study.

170 The empirical relationships between foraminiferal growth rates and abundances in the FORAMCLIM

171 model were originally calibrated against a compilation of multinet plankton tow data (Watkins *et al.*,

172 1996; Watkins *et al.*, 1998; Schiebel *et al.*, 2001; Field, 2004; Kuroyanagi & Kawahata, 2004;

173 Schiebel *et al.*, 2004), which is why we can't use this database to evaluate the model. We use the

174 sampling sites from this same data set to characterize the carbonate chemistry of the present-day

175 potential habitat of foraminiferal species. Here we "sample" the observed calcite saturation state, Ω_C,

176   at the same locations (latitude, longitude, depth; Figure S2b) where foraminifera have been collected

177   in multinet plankton tows (Watkins *et al.*, 1996; Watkins *et al.*, 1998; Schiebel *et al.*, 2001; Field, 2004;

178   Kuroyanagi & Kawahata, 2004; Schiebel *et al.*, 2004). Ω_C is calculated based on the GLODAP (Key

179   *et al.*, 2004) and WOCE (World Ocean Circulation Experiment) databases. For each species of

180   foraminifera we estimate the percentage of the abundance residing in waters of different Ω_C ranges.

181   *2.4. Model performance*

182   The FORAMCLIM model captures the broadscale patterns of abundance and species dominance.

183   The distributions of surface abundance from plankton tows (Bé & Tolderlund, 1971) are well captured

184   by the model with the highest abundances in the tropics and subpolar regions and the lowest in the

185   subtropics (Figure S3a). Yet, surface abundances tend to be overestimated, particularly in the

186   subtropics. This is most likely due to the model being calibrated against multinet plankton tow data,

187   which uses smaller mesh sizes (63–100 μm) relative to the 200 μm used by Bé & Tolderlund (1971).

188   Qualitatively, the dominant species (the species with the highest abundance) were also simulated well

189   by the model with *G. bulloides* in the more productive upwelling areas and temperate zones, *G. ruber*

190   in the subtropical gyres, *N. pachyderma* in the subpolar/polar regions and *G. sacculifer* dominating in

191   the tropical/subtropical regions in between (Figure S3). The model reproduced 43% of the observed

192   species dominance from surface plankton tow data (Table 2). This level of agreement is lower than

193   the model-based and satellite-based estimates of Lombard *et al.* (2011) (Table 2) and is most likely

194   due to the displacement of the simulated water masses and oceanic fronts relative to their real world

195   counterparts, as is typical of Earth system models (Seferian *et al.*, 2013). Also some species have

196   quite similar abundances locally, so small errors in abundance can lead to significant errors in species

197   dominance.

198   The relative abundances and diversity are well captured by the model with the relative abundance

199   root mean square errors (RMSE) ranging between 3.2% and 24.1% and a diversity RMSE of 0.48

200   (Table 2). For all species, expect *N. pachyderma*, the relative abundance RMSEs are slightly larger

201   than in Lombard *et al.* (2011), but smaller than in Fraile *et al.* (2008).

202   In summary, there is a tendency to slightly overestimate the standing stock of foraminifera relative to

203   the sparse surface plankton data, and to underestimate the changes in abundance in response to

204   changing environmental conditions relative to observed abundances from sediment cores (Kageyama

205   *et al.*, 2012).

206   *2.1. Modelling planktonic foraminifera: strengths and limitations*

207   The two most established approaches currently used to simulate the biodiversity of foraminifera are

208   the ecophysiological approach used in this study, FORAMCLIM (Lombard *et al.*, 2011), and the

209   ecosystem approach developed specifically to capture dynamic changes in planktonic foraminiferal

210   populations, PLAFOM (Fraile *et al.* 2008). All approaches used for projecting climate impacts on

211   marine biogeography have their unique set of strengths and weaknesses (Pereira *et al.*, 2010). One

212   of the drawbacks of the dynamic ecosystem approach is that many processes (i.e. mortality,

213   competition, and predation) are not well known (Hemleben *et al.*, 1989). Furthermore, the parameters

214   that describe these processes can't be optimized independently using the data that is currently

215   available. Another limitation of the Fraile *et al*. (2008) approach is that the depth profiles of

216   foraminiferal abundance are not simulated. Capturing vertical changes is important if we want to

217   estimate the impact of shifts in habitat preference on both the net foraminiferal abundance and the

218   climate signals recorded by foraminiferal paleoproxies. Yet, the dynamical approach could be better

219   adapted to simulate events controlled by population biology and hydrodynamics, which are known to

220   be important in controlling foraminifera abundance and their flux to the deep ocean (De La Rocha &

221   Passow, 2007), such as the pulsed fluxes of foraminiferal tests that can occur sporadically (Sautter &

222   Thunell, 1991) or in short bursts in response to storms (Schiebel *et al.,* 2005), and the advection of

223   empty tests from their production sites (Siegel & Deuser, 1997; von Gyldenfeldt *et al.*, 2002).

224   One of the attractive aspects of the FORAMCLIM model is that it is empirically-based. The

225   relationships between environmental conditions (i.e. light, temperature) and foraminiferal growth rates

226   are derived under controlled laboratory conditions. Since it is impossible, based on the available

227   knowledge, to incorporate the influence of all ecological and physiological processes on foraminiferal

228   abundance, the relationships between growth rates and abundance are calibrated against the

229   standing stock of foraminifera from multinet plankton tows; effectively allowing us to bridge this

230 sizeable knowledge gap. The parameters of this calibration integrate the influence of the processes

231 unresolved by the model. By applying the foraminifera model to climate simulations we can project

232 these observation-based relationships into the future.

233 Critical to reliable model performance is that these model relationships are realistic. Here we

234 elaborate on a previous discussion of the strengths and limitations of the FORAMCLIM model

235 (Lombard *et al.*, 2011). First, the laboratory-based growth rate relationships may not hold for the real

236 ocean. The laboratory experiments were conducted on specific specimens whose response to

237 environmental perturbations may not be representative of the global population—similar to the

238 responses that have been observed for different strains of coccolithophore species in response to

239 changes in carbonate concentration (Ridgwell *et al.*, 2009; Langer *et al.,* 2009). Also, foraminifera in

240 the laboratory could be more sensitive to perturbations in environmental conditions than in their

241 natural habitat. It hasn't been possible to reproduce planktonic foraminifera in the laboratory, which is

242 one indication that foraminifera in the laboratory are not behaving as they would in their natural

243 environment. Furthermore, the physiological responses of foraminifera in the laboratory could be

244 more related to stress than to environmental perturbations. It is important to keep in mind that

245 although all physiological laboratory experiments are artificial, they are currently the most direct

246 approach available for quantifying the growth response of foraminifera to specific environmental

247 changes.

248 Another potential weakness is that the relationships between the abundances and the growth rates

249 are weakly correlated (Lombard *et al.*, 2011). This could partly be due to each morphological species

250 being a combination of cryptic species, each with distinct habitat preferences and responses to

251 environmental change (de Vargas *et al.*, 2002). A convincing explanation for the weak relationship

252 between biomass and abundance could be related to the FORAMCLIM model not resolving variations

253 in shell size: a wide range of abundances can be fitted to the same total biomass of a foraminiferal

254 population depending on how this biomass is distributed over different size classes. To illustrate this

255 point, we can take the typical biomass size spectrum from Schiebel and Mollevan (2012): a 1 m^3 of

256 water with a foraminiferal abundance of 100 individuals m^{-3} is grouped into 3 size classes 100–150

257 μm, 150–250 μm, and 250+ μm with each size class having 75, 19 and 6 individuals respectively. A

258 small change in the size spectrum (e.g. having just two more individuals in the largest and

259   intermediate size classes (i.e. 21, 8 individuals each) would require a large decrease in the total

260   abundance from 100 to 68 individuals to match the same total biomass.

261   Another limitation of the FORAMCLIM model is that it currently includes only the species on which

262   sufficient physiological laboratory experiments have been conducted. That is, 8 of the approximately

263   50 species of morphologically-distinct planktonic foraminifera. Therefore, it can't be used to estimate

264   the total (i.e. all species) foraminiferal abundance, diversity or carbonate production. Nevertheless,

265   based on sediment top-core samples (Kucera et al., 2004), the 8 species currently represented in the

266   FORAMCLIM model account for a large proportion of the total abundance (about 50%).

3. Results

3.1. Future changes in abundance and diversity

269   Under climate change, temperature, food availability and light were perturbed such that the total

270   foraminiferl abundance (combined abundance of the eight species in the FORAMCLIM model, Figure

271   1a) shifted polewards from the tropics to the subtropics, while abundance decreased in the subpolar

272   regions (Figure 1b) by the end of the century. The simulated depth-integrated abundance reduced by

273   up to 40% in the tropics and subpolar regions and increased by greater than 100% in the subtropics.

274   Throughout the tropics the total abundance (Figure 1c) shifted deeper in the water column (Figure

275   1d), reducing the total abundance of foraminifera at the ocean surface by more than 50% (>10 ind m^{-}

276   ^{3}, Figure 2b). Under climate change the pattern of foraminiferal diversity (Figure 2c) responded

277   similarly to that of abundance: it decreased in the tropics, increased in the subpolar regions (Figure

278   2d) and shifted to depth in the tropics (not shown). The decreased diversity in the tropics is primarily

279   due to the local disappearance of *G. siphonifera* and *N. dutertrei*.

280   In the simulation, three species dominated the changes in total foraminiferal abundance: the two

281   abundant warm-water species—*G. ruber* and *G. sacculifer*—drove the reduction in total abundance in

282   the tropics and the increase in the subtropics, while *N. pachyderma* dominated the reduction in the

283   high latitudes and the small increases in abundance around the poles (Figures 3a and 3b). In the

284   tropics, the climate-driven reductions in the distribution of *G. ruber* and *G. sacculifer* were similar in

285   magnitude (5 ind m^{-3}), and each integrated to a more than 100 ind m^{-2} reduction over the whole water

286   column (Figure 3b). In the high-latitudes, the poleward shift in abundance of *N. pachyderma* reduced

287   the net abundance in surface waters (~4 ind m^{-3}) and throughout the water column (~200 ind m^{-2}, not

288   shown).

289   The changes in relative abundance are also presented, since this is what is measured in sediment

290   cores. In the tropics, despite the large decreases in the abundances of the two dominant species (*G.*

291   *ruber* and *G. sacculifer*), their relative abundances at the ocean surface increased (Figure 3c) and the

292   depth-integrated relative abundances changed very little (Figure 3d). In the mid latitudes (10°–40°)

293   the abundance and relative abundance of *G.bulloides, N. incompta* and *N. dutertrei* decreased, while

294   *G. sacculifer* and *G. ruber* increased. In the high latitudes (>50°), where the species diversity is much

295   lower than in the tropics (Figure 2c), the changes in abundance resulted in changes in the relative

296   abundance that can interpreted more easily. Although the abundance of *G.bulloides*, *N. incompta* and

297   *N. dutertrei* barely changed (Figure 3a and 3b), the large decrease in the abundance of the dominant

298   species, *N. pachyderma,* drove a substantial increase in the relative abundance of these species

299   (Figure 3c and 3d). The more even distribution of abundance between the species resulted in an

300   overall increase in the diversity index in the higher latitudes (Figure 2d).

301   *3.2. Environmental drivers of foraminiferal biogeography*

302   It is not directly possible to separate the impact of temperature and food on foraminiferal distributions

303   in nature, so we turn to the model to attempt to explore the potential relative impacts of projected

304   changes in food, temperature and light on future foraminiferal distributions. An advantage of the

305   FORAMCLIM model is the ease with which the various drivers of the changes in abundance can be

306   disentangled. By systematically allowing only one parameter to vary, we can partially separate the

307   total change in foraminiferal abundance into components driven by each of the environmental

308   drivers—temperature, food and light. Given the paucity of data for the evaluation of these simulated

309   responses, these results should be regarded as initial sensitivity experiments. The future change in

310   ocean temperature (Figure 4) is the primary driver of the change in the basin-scale biogeography of

311   foraminifera (Figure 5), followed by food availability (Figures 4,5). Changes in light availability have a

312   minor impact (not shown).

313   Temperature was the dominant driver of the poleward shift of foraminiferal abundance from the

314   tropics (Figure 5a). The 1–3°C increase in sea surface temperatures in the tropics and subtropics

315   (Figure 4a) throughout the water column (Figure 4b) decreased the habitat suitability in the tropical

316   waters—the waters became too warm for optimal foraminiferal growth—yet increased the habitat

317   suitability in the subtropics (Figure 5a) and in the deeper waters of the tropics (Figure 5b).

318   In the subpolar and polar regions, where *N. pachyderma* dominates (Figure 3a,b), the shift in

319   abundance was a combined response to temperature and food-driven changes in nutrition rates

320   (Figure 5a and 5c respectively). The broadscale patterns, the subpolar decrease and polar increase in

321   abundance (Figure 5a,b), were driven by temperature (Figure 4a). Yet, increases in phytoplankton

322   concentration in localized patches, particularly in the Southern Ocean (Figure 4c), and in subsurface

323   waters (Figure 4d) drove increases in abundance (Figures 5c and 5d). The increase in phytoplankton

324   abundance in the Southern Ocean is a shared feature of many future climate change simulations and

325   is explained by the alleviation of light and iron limitation on phytoplankton growth (Steinacher et al.,

326   2010). The food-driven increases in the foraminiferal abundance tended to offset the temperature-

327   driven reductions. Other areas with similar offsets include large patches throughout the North Atlantic

328   and the Equatorial and coastal upwelling regions.

329   *3.3. Species abundance and potential suitable habitat*

330   To assess the species-specific vulnerability of foraminifera to climate change we calculated the

331   percent change in the globally-averaged species abundance and potential suitable habitat (Figure 6),

332   where the potential habitat is defined as anywhere where the environmental conditions (i.e.

333   temperature, food and light conditions) are sufficient for foraminiferal growth. Some species 'profited'

334   (*O. universa*, *G. sacculifer*, *G. siphonifera* and *G. ruber*); that is their potential habitat increased by

335   between 5% and 20%. Whilst higher-latitude species were more vulnerable (e.g. *N. incompta*, *N.*

336   *pachyderma*): their potential habitat and net abundance decreased by between 10% and 40%. For *G.*

337   *siphonifera* the potential habitat increased but the abundance decreased.

3.4. Carbon chemistry of the foraminiferal habitat

339 Although we don't explicitly account for the impact of ocean acidification on either foraminiferal

340 calcification or physiological processes in the current version of the FORAMCLIM model, we can

341 make an assessment of the potential impacts by quantifying the predicted changes in the carbonate

342 concentration $[CO_3]^{2-}$ and calcite saturation state, Ω_C, within the habitat range of each species of

343 foraminifera.

344 First, we would like to have an indication of the present-day distribution of foraminiferal abundance

345 within waters of different Ω_C classes. We find that only a very small proportion of the abundance of all

346 the foraminiferal species resides in waters with Ω_C less than 2, even though substantial volumes of

347 water with low Ω_C are sampled, particularly in the northern high latitudes (Figure 7). The highest

348 foraminiferal abundances from the multinet plankton tows were sampled in waters with $3 < \Omega_C < 6$.

349 Second, we project how the carbonate chemistry of foraminiferal habitat changes by the end of this

350 century. Calcite saturation states decrease throughout the global ocean and waters with low

351 saturations states ($\Omega_C < 2$) shoal (Figure 8a,b) and become more widespread across the surface

352 ocean. Most surface waters polewards of 40° have $\Omega_C < 2$. Virtually none of the simulated present-

353 day foraminiferal habitat has ambient $\Omega_C < 2$. Yet, by the end of the century between 10% and 95% of

354 the habitats of most foraminiferal species have an $\Omega_C < 2$ (Figure 8c). High latitude species, *N.*

355 *pachyderma* and *N. incompta*, are potentially most vulnerable, with some of their suitable habitat even

356 becoming undersaturated ($\Omega_C < 1$) with respect to calcite by the end of the century (when Ω_C is below

357 the threshold of $\Omega_C = 1$, mineral calcite becomes unstable). Also, the carbonate ion concentrations of

358 the potential foraminiferal habitat decrease to between 20 and 70 μmol kg^{-1}, with the largest

359 reductions in the equatorial regions (Figure 8d).

4. Discussion

4.1. Climate impacts

It is unclear how vulnerable specific foraminiferal species may be to anthropogenic climate change. Since the last substantial extinction event in the Pliocene the modern assemblage of species has remained relatively stable under glacial-interglacial fluctuations (Jackson & Sheldon, 1994). Yet, the oceanic environment is fast approaching conditions that are well outside those of glacial-interglacial cycles. It is expected that pelagic species, and in particular planktonic species, will have the potential to escape some climatic changes by shifting their populations to regions with more favorable conditions (Burrows *et al.*, 2011), as predicted here for species such a *G. sacculifer* and *G. ruber*. Yet, we show that the available potential habitat is reduced for high latitude species, such as *N. pachyderma*, and that this reduction is associated with a drop in the net global abundance. For one species, *G. siphonifera*, the suitable habitat range increases, yet it's net global abundance decreases. Such an increase in habitat range without similar increases in abundance indicates that temperature, light and food availability are perturbed such the species can exist over a greater habitat range, but that the overall environmental conditions are suboptimal for foraminiferal growth.

Based on the FORAMCLIM simulations, it would be expected that anthropogenically-driven shifts in the basin-scale biogeography of foraminifera should be observable (Figure 3 a,b). But, in sediment samples, the changes in the relative abundances in some regions, particularly the tropics, may be too small to detect (Figure 3d). Furthermore, shifts in the species abundance can cause non-intuitive shifts in the relative abundance, particularly in regions of high species diversity such as the tropics. Yet, in the high latitudes, where the diversity is lower (Figure 2d), the interpretation of the changes in relative abundance should be simpler.

We have shown that climate change is projected to alter the temperature, food and light conditions that influence foraminiferal growth rates and, consequently, shift both the vertical and geographical distributions of foraminiferal abundance/diversity (Figures 1 & 2). In the tropics/subtropics, the changes in abundance are driven by the regionally dominant species: *G. ruber* and *G. sacculifer*. Here, temperature (Figure 4) dominates the geographical shifts in foraminiferal abundance, while

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387   multiple drivers (phytoplankton and temperature) cause the vertical shifts (Figure 5). On the contrary,

388   in the polar/subpolar regions food availability and temperature drive the geographical shifts in

389   foraminiferal abundance, while mostly changes in phytoplankton concentrations drive the vertical

390   shifts. The changes in the abundance of foraminifera are associated with *N. pachyderma* and are in

391   agreement with observational studies (Fairbanks & Wiebe, 1980; Kohfeld *et al.*, 1996; Kuroyanagi &

392   Kawahata, 2004; Bergami *et al.*, 2009) that demonstrate that the geographical distribution was

393   primarily controlled by ocean temperatures, while the vertical distribution was controlled by the depth

394   of the chlorophyll maximum and the pycnocline. Light doesn't produce a strong change in abundance

395   in our simulations and is therefore not discussed here. In reality, however, the response of symbiont-

396   bearing foraminifera to light is likely to be much more complex than simulated in the foraminifera

397   model.

398   The drivers of vertical and horizontal distributional changes can differ because food, light and

399   temperature may have impacts on foraminiferal abundances that are uncorrelated: they either act to

400   reinforce or counteract each other's impact on foraminiferal abundances. Also, the drivers themselves

401   may not be well correlated. Under climate change, Earth system models simulate increases in ocean

402   temperature in most regions, yet PP can either decrease or increase (Steinacher et al., 2010).

403   Furthermore, the nutritional requirements of each species is unique representing the different

404   strategies that foraminifera use to feed and grow. Symbiotic species have a strong dependence on

405   light availability. Therefore they mostly display horizontal effects and vertical shifts that are restricted

406   to the euphotic zone (up to about 200 m). Species without symbionts can display less restricted

407   vertical responses because they don't rely directly on light. They can travel as deep as the food

408   source. Species with a stronger prey dependency are more likely to be more sensitive to changes in

409   the availability of prey than temperature. This complexity is taken into account in the

410   ORCA/PISCES/FORAMCLIM models. For example, in the high latitudes, the dominant species here,

411   *N. pachyderma*, drives much of the change in the simulated total foraminiferal abundance. It's

412   abundance is reduced throughout most of it's habitat range in response to a warming ocean, but it's

413   abundance increases over patches of the ocean, and shifts to depth in some regions, in response to

414   an increase in food availability. By contrast, in tropics/subtropics the dominant species G. sacculifer

415   and G. ruber shift polewards and deeper in the water column both as the thermocline and nutricline

416   deepen, yet food availability does not contribute to the latitudinal shifts because the column-integrated

417   food availability is not altered significantly throughout the habitat range.

418   We show that climate change could result in vertical shifts in foraminiferal abundance that are driven

419   by either or both food availability and temperature. Interestingly, comparable vertical shifts in

420   foraminiferal abundance over glacial-interglacial time periods may complicate the reconstruction of

421   sea-surface temperatures from foraminiferal microfossil deposits: in paleoclimate reconstructions the

422   vertical distributions foraminifera are generally assumed to be stationary over time (e.g. Kucera et al.,

423   2005).

424   Opinions differ on the relative impacts of food availability, temperature or other environmental factors

425   on the distribution of planktonic foraminifera. Although it is generally accepted that at the extremes of

426   a species temperature tolerance, temperature drives the changes in the geographical extent of

427   foraminifera (Rutherford *et al.*, 1999), each species' preferred temperature range is broad. Within

428   these temperature ranges it has been shown that regional patterns of abundance are strongly

429   correlated with specific-specific responses to food, light (Ortiz *et al.*, 1995; Watkins *et al.*, 1996; Field,

430   2004) salinity, and turbidity (Retailleau *et al.*, 2011). On the contrary, it could be argued that food

431   availability is generally adequate to maintain foraminiferal populations and that changes in abundance

432   are primarily temperature-driven. A database of time series of abundance/assemblage data and

433   concomitant environmental measurements of temperature, food and light would be an invaluable

434   resource for the evaluation of the drivers of the simulated changes in the distributions of foraminiferal

435   abundance.

436   The simulated response of foraminiferal diversity to climate change may differ significantly if all extant

437   species could be included in the model. For example, tropical species present in low concentrations,

438   but excluded in this analysis, could flourish as temperatures increase. Also, the vertical stratification of

439   large regions of the global ocean should increase with climate change (Sarmiento *et al.*, 2004), which

440   can increase vertical niche separation thereby allowing a greater diversity of species to subsist (Al-

441   Saboui *et al.*, 2007). By including more species in the FORAMCLIM model, these effects could

442   counteract the simulated decrease in diversity in the tropics. Another important factor that will

443   influence how diversity responds to climate change is that most foraminiferal morphospecies have

444 many genotypes that exhibit specific ecology, habitat preferences and biogeography (Aurahs *et al.*,

445 2009). A potential approach to incorporate more species diversity, and to partially circumvent the lack

446 of information on key ecological and physiological processes for many foraminiferal species, would be

447 to apply the self-assembling biodiversity approach (Follows et al., 2007) to simulate more complex

448 foraminiferal assemblages.

449 *4.2. Calcification and acidification impacts*

450 If net calcification were to scale directly with foraminiferal abundance, the large-scale rearrangements

451 in abundance with climate change would alone cause significant changes in regional carbonate

452 production. For example, in the tropics/subtropics the 40% decrease in total simulated foraminiferal

453 abundance could produce a 20% reduction in total planktic foraminiferal carbonate production, given

454 that the 8 species in the FORAMCLIM model account for about 50% of the total planktonic

455 foraminiferal abundance observed in the sediment core-tops (Kucera *et al.,* 2004). Such population–

456 driven impacts on carbonate production could be further amplified or dampened if calcification rates

457 themselves are impacted by anthropogenic change. Ocean acidification and the associated decrease

458 in carbonate ion concentrations can alter foraminiferal calcification rates (Lombard *et al.* 2010; Keul *et*

459 *al.,* 2013), while higher ocean temperatures could accelerate calcification rates within certain

460 temperature windows.

461 With future increases in atmospheric CO_2, we show that the carbonate concentration of the preferred

462 habitat range of planktonic foraminifera decreases zonally from 10–30 μmol kg^{-1} in the polar/subpolar

463 regions to 30–70 μmol kg^{-1} in the subtropical/tropical regions by the end of this century (Figure 8d).

464 Even without dropping below the calcite saturation state, such changes in carbonate ion concentration

465 may have significant impacts on foraminiferal tests. Evidence exists for shell thinning in foraminifera

466 over recent (de Moel *et al.*, 2009; Moy *et al.*, 2009) and geological timescales (Barker & Elderfield,

467 2002) and it has been suggested that these changes are a response to higher atmospheric CO_2

468 concentrations and the reduction of carbonate ion concentrations (Keul *et al.,* 2013). Such as for other

469 calcifying planktonic species (Riebesell *et al.*, 2000; Zondervan *et al.*, 2001; Fabry *et al.*, 2008;

470 Comeau *et al.*, 2010), the calcification by foraminifera is sensitive to changes in the carbonate ion

471 concentration both in their natural environment (Beer *et al.*, 2010) and in laboratory cultures (Spero *et*

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472   *al.*, 1997; Bijma *et al.*, 1999; Bijma *et al.*, 2002; Russell *et al.*, 2004; Beer *et al.*, 2010; Lombard *et al.*,

473   2010; Manno *et al.*, 2012; Keul *et al.,* 2013).

474   Despite the uncertainties associated with foraminiferal calcification, it is interesting to have a sense of

475   the magnitude of the change in calcification that could be expected by applying laboratory-derived

476   relationships (i.e. calcification vs carbonate ion concentration) from the literature to the foraminiferal

477   distributions and the carbonate ion concentrations simulated here. For example, in a series of

478   laboratory experiments, a reduction of 30–40 μmol kg^{-1} in the carbonate ion concentration was

479   associated with a 21–30% reduction in the calcification rates of *N. pachyderma* (Manno *et al.*, 2012).

480   The reduction in the carbonate ion concentration throughout the habitat of *N. pachyderma* is projected

481   to be ~30 μmol kg^{-1} (Figure 8d) and by crude extrapolation, we could expect a similar >20% drop in

482   the net *N. pachyderma* foraminiferal carbonate flux in the high-latitudes due to ocean acidification by

483   the end of this century. This reduction would reinforce the reduction in carbonate production due to

484   the net climate-driven decrease in abundance of this species throughout its habitat range (Figures 3b,

485   6). Similarly, based on the observed changes in the calcification rates of *G. sacculifer* with carbonate

486   ion concentration (Bijma *et al.*, 2002; Lombard *et al.*, 2010, see equation 3), the projected reduction of

487   up to 70 μmol kg^{-1} in the carbonate ion concentration in the tropical/subtropical habitat range of *G.*

488   *sacculifer* (Figure 8d) could result in an up to 10% reduction in the calcification rates of this species.

489   Again, this would reinforce the reduction in carbonate production associated with the decrease in the

490   abundance of this species throughout the tropics (Figure 3b), yet would counteract the increase in

491   carbonate production associated with enhanced abundance in the subtropics.

492   In the polar/subpolar regions *N. pachyderma* dominates the assemblages (Figure S3b). The tests of

493   *N. pachyderma* are expected to be most vulnerable to dissolution because the polar regions have

494   lower carbonate ion concentrations and are consequently closer to the threshold of calcite saturation

495   (Ω =1). We show that by the end of the century, most of the habitat of high-latitude species drops

496   below the calcite saturation state of 2 with greater than 10% of the potential habitat of the dominant

497   high-latitude species, *N. pachyderma*, residing below the saturation horizon (Figure 8c), which could

498   result in shell dissolution throughout this range.

499   Although calcification by foraminifera is directly influenced by CO_3^{2-}, many other environmental factors

500   besides ambient carbonate ion concentrations influence the shell weight (de Villiers, 2004) including

501   temperature (Hemleben *et al.*, 1989; Manno *et al.*, 2012), light (Spero, 1992; Lombard *et al.*, 2010),

502   growth potential (Aldridge *et al.*, 2012). Clearly, the environmental controls on calcite production by

503   foraminifera are still poorly understood. A complex intra- and interspecies-specific interplay of factors

504   drive foraminiferal shell weights (Beer *et al.*, 2010). Both the magnitude and the sign of the slope of

505   the relationships between shell weight and carbonate ion concentrations vary between and within a

506   species (Keul *et al.,* 2013) and they vary widely depending on whether the relationships were based

507   on plankton tows (Beer *et al.*, 2010), top core sediments (Barker & Elderfield, 2002), or laboratory

508   cultures (Bijma *et al.*, 1999; Bijma *et al.*, 2002). A quantitative assessment of the impact of

509   acidification on the foraminiferal carbonate flux can be made with confidence only once these

510   complexities have been taken into account.

511   To quantify the foraminiferal carbonate flux, further model development should be encouraged,

512   particularly the incorporation of enhanced species diversity, shell calcification processes, and

513   empirical relationships between environmental conditions and foraminiferal size. Ideally, future

514   models will also incorporate the physiological response of foraminiferal calcification to multiple

515   environmental drivers.

516   *4.3. Future challenges*

517   The challenge remains to observationally evaluate how well foraminifera models capture changes in

518   abundance in response to environmental change. There is little large-scale observational evidence for

519   historical trends in foraminiferal abundance and diversity over the period of anthropogenic climate

520   change. Large-scale changes in foraminiferal abundance have been observed in continuous plankton

521   records over the last five decades in the North Atlantic that are intriguingly similar to our simulations

522   (McQuatters-Gollop *et al.*, 2010), with large increase in the frequency of occurrence between 40°N

523   and 60°N. But further analysis of this data set is required before a quantitative assessment can be

524   made. Changes in species composition in response to anthropogenic climate change have been

525   observed in the sediment record of the Santa Barbara basin (Field *et al.*, 2006). It was shown that

526 historical warming trends were associated with an increase in the abundance of tropical/subtropical

527 species, and a decrease in subpolar/polar species (i.e. *N. pachyderma*) over the 20th century.

528 Ideally, the FORAMCLIM simulations should be tested against present-day time series of planktonic

529 abundance and the key environmental variables such as temperature, phytoplankton concentration

530 and light. For future studies, there are several instrumental records that should become available and

531 provide an invaluable resource to improve our understanding of the environmental controls on the

532 biogeography of foraminifera, including data collected with: i) plankton tows, ii) sediment traps (Zaric

533 *et al.*, 2005), iii) sediment cores, and iv) continuous plankton recorders (CPR).

534 The plankton tow data used here for the construction of the empirical relationships between

535 physiological growth rates and abundances, represent only a subsample of what should become

536 available in the future. More studies of historical trends in the assemblage of planktonic foraminifera

537 deposited in ocean sediments, such as that of Field et al., (2006), would be invaluable for evaluating

538 the longer-term responses of species assemblages to climate change. Yet, such studies are restricted

539 to ocean sediment cores from locations with high sedimentation rates and sufficient temporal

540 resolution to determine historical trends. These would not be expected to provide the spatial coverage

541 required for the basin-scale evaluation of global models. CPR records provide long time series of

542 plankton diversity, yet unfortunately, we found that the routine preservation protocol used to store

543 CPR samples did not preserve foraminifera well enough to determine relative abundances or shell

544 weights. Only the most robust individuals were preserved and even their shells were found to be

545 brittle and difficult to speciate. Another potential complication with foraminiferal CPR data is that the

546 sample may not represent the mean surface ocean distribution of foraminifera because i) the CPR

547 does not resolve different water depths, and ii) the large mesh size (>200 μm) means that the smaller

548 fraction of the foraminiferal fauna is not captured in the samples. Nevertheless, by taking the statistics

549 of the CPR sampling protocol into account, it should be possible to use the total abundance of

550 foraminifera recorded in the original written records for each CPR sample to evaluate the simulated

551 changes in total foraminiferal abundance from the model.

552 Sedimentary paleorecords over glacial/interglacial timescales may be useful analogs for historical

553 climate change. Yet, it can be difficult to know which combination of species is driving the observed

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554 changes in relative abundance. The differential dissolution of foraminifera in the sediments further

555 complicates the interpretation of the signals recorded here. Also, we don't have direct measurements

556 of the key environmental drivers of foraminiferal abundance — temperature, light, food availability—

557 back through time, and must draw on proxy-based estimates of these quantities, which are plagued

558 by similar uncertainties, and the proxies themselves are often based on foraminifera.

559 Improved skill in representing the simulated responses of foraminiferal growth and abundance to

560 environmental change and variability in models will increase our confidence in both future projections

561 of foraminiferal biogeography and the reconstructions of past climates. Subsequent studies should

562 focus on i) the continued sampling of foraminiferal diversity, abundance, and shell size and

563 concomitant biophysical parameters to quantify changes in their distributions in response to

564 environmental perturbations, and ii) evaluating the detectability of large-scale biogeographical shifts

565 driven by climate-change given the natural variability in foraminiferal distributions. Given that the

566 distributions of foraminifera are one of the most well known of all the taxa in the pelagic ocean and the

567 feasibility of monitoring the large-scale changes in foraminifera, we have confidence that ongoing

568 model-data syntheses should lead to detection and attribution of anthropogenically-driven changes in

569 large-scale planktonic foraminiferal distributions.

5. References

571 Al-Saboui N, Kucera M, Schmidt DN (2007) Vertical niche separation control of diversity and size

572   disparity in planktonic foraminifera. *Marine Micropaleontology,* **63**, 75-90.

573 Aldridge D, Beer CJ, Purdie DA (2012) Calcification in the planktonic foraminifera Globigerina

574   bulloides linked to phosphate concentrations in surface waters of the North Atlantic Ocean.

575   *Biogeosciences,* **9**, 1725-1739.

576 Anderson LA, Sarmiento JL (1994) Redfield ratios of remineralization determined by nutrient data

577   analysis. *Global Biogeochemical Cycles,* **8**, 65-80.

578 Aumont O, Bopp L (2006) Globalizing results from ocean in situ iron fertilization studies. *Global

579   Biogeochemical Cycles,* **20**.

580   Aumont O, Maier-Reimer E, Blain S, Monfray P (2003) An ecosystem model of the global ocean

581   including Fe, Si, P colimitations. *Global Biogeochemical Cycles,* **17**.

582   Aurahs R, Grimm GW, Hemleben V, Hemleben C, Kucera M (2009) Geographical distribution of

583   cryptic genetic types in the planktonic foraminifer Globigerinoides ruber. *Molecular Ecology,*

584   **18**, 1692-1706.

585   Barker S, Elderfield H (2002) Foraminiferal calcification response to glacial-interglacial changes in

586   atmospheric CO_2. *Science,* **297**, 833-836.

587   Barker S, Higgins JA, Elderfield H (2003) The future of the carbon cycle: review, calcification

588   response, ballast and feedback on atmospheric CO_2. *Philosophical Transactions of the Royal*

589   *Society of London Series a-Mathematical Physical and Engineering Sciences,* **361**, 1977-

590   1998.

591   Barrows TT, Juggins S (2005) Sea-surface temperatures around the Australian margin and Indian

592   ocean during the last glacial maximum. *Quaternary Science Reviews,* **24**, 1017-1047.

593   Bé AWH, Tolderlund DS (1971) *6. Distribution and ecology of living planktonic foraminifera in surface*

594   *waters of the Atlantic and Indian oceans, in: Micropaleontology of oceans.,* London, UK,

595   Cambridge University Press.

596   Beer CJ, Schiebel R, Wilson PA (2010) Testing planktic foraminiferal shell weight as a surface water

597   CO32- proxy using plankton net samples. *Geology,* **38**, 103-106.

598   Bergami C, Capotondi L, Langone L, Giglio F, Ravaioli M (2009) Distribution of living planktonic

599   foraminifera in the Ross Sea and the Pacific sector of the Southern Ocean (Antarctica).

600   *Marine Micropaleontology,* **73**, 37-48.

601   Berger WH, Piper DJW (1972) Planktonic foraminifera - differential settling, dissolution, and

602   redeposition. *Limnology And Oceanography,* **17**, 275–287.

603   Bijma J, Faber WW, Hemleben C (1990) Temperature and salinity limits for growth and survival of

604   some planktonic foraminifers in laboratory cultures. *Journal of Foraminiferal Research,* **20**,

605   95-116.

606   Bijma J, Hemleben C, Oberhansli H, Spindler M (1992) The effects of increased water fertility on

607   tropical spinose planktonic foraminifers in laboratory cultures. *Journal of Foraminiferal*

608   *Research,* **22**, 242-256.

609 Bijma J, Honisch B, Zeebe RE (2002) Impact of the ocean carbonate chemistry on living foraminiferal

610   shell weight: Comment on "Carbonate ion concentration in glacial-age deep waters of the

611   Caribbean Sea" by W. S. Broecker and E. Clark. *Geochemistry Geophysics Geosystems,* **3**.

612 Bijma J, Spero HJ, Lea DW (1999) Reassessing foraminiferal stable isotope geochemistry: Impact of

613   the oceanic carbonate system (experimental results). In: *Use of Proxies in*

614   *Paleoceanography: Example from the South Atlantic.* (eds Fischer G, Wefer G). New York,

615   Springer-Verlag, pp 489–592.

616 Buitenhuis ET, Vogt M, Moriarty R *et al.* (2013) MAREDAT: towards a World Ocean Atlas of MARine

617   Ecosystem DATa. *Earth System Science Data Discussions,* **5**, 1077-1106.

618 Burrows MT, Schoeman DS, Buckley LB *et al.* (2011) The Pace of Shifting Climate in Marine and

619   Terrestrial Ecosystems. *Science,* **334**, 652-655.

620 Comeau S, Jeffree R, Teyssie JL, Gattuso JP (2010) Response of the Arctic Pteropod Limacina

621   helicina to Projected Future Environmental Conditions. *Plos One,* **5**.

622 De La Rocha CL, Passow U (2007) Factors influencing the sinking of POC and the efficiency of the

623   biological carbon pump. *Deep-Sea Research Part Ii-Topical Studies In Oceanography,* **54**,

624   639-658.

625 de Moel H, Ganssen GM, Peeters FJC, Jung SJA, Kroon D, Brummer GJA, Zeebe RE (2009) Planktic

626   foraminiferal shell thinning in the Arabian Sea due to anthropogenic ocean acidification?

627   *Biogeosciences,* **6**, 1917-1925.

628 de Vargas C, Bonzon M, Rees NW, Pawlowski J, Zaninetti L (2002) A molecular approach to

629   biodiversity and biogeography in the planktonic foraminifer Globigerinella siphonifera

630   (d'Orbigny). *Marine Micropaleontology,* **45**, 101-116.

631 de Villiers S (2004) Optimum growth conditions as opposed to calcite saturation as a control on the

632   calcification rate and shell-weight of marine foraminifera. *Marine Biology,* **144**, 45-49.

633 Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and

634   ecosystem processes. *Ices Journal of Marine Science,* **65**, 414-432.

635 Fairbanks RG, Sverdlove M, Free R, Wiebe PH, Be AWH (1982) Vertical-distribution and isotopic

636   fractionation of living planktonic-foraminifera from the Panama basin. *Nature,* **298**, 841-844.

637 Fairbanks RG, Wiebe PH (1980) Foraminifera and chlorophyll maximum - vertical-distribution,

638   seasonal succession, and paleoceanographic significance. *Science,* **209**, 1524-1526.

639   Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., & Millero, F. J. (2004).

640   Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science, **305**(5682), 362–

641   366.

642   Field DB (2004) Variability in vertical distributions of planktonic foraminifera in the California Current:

643   Relationships to vertical ocean structure. *Paleoceanography,* **19**.

644   Field DB, Baumgartner TR, Charles CD, Ferreira-Bartrina V, Ohman MD (2006) Planktonic

645   foraminifera of the California Current reflect 20th-century warming. *Science,* **311**, 63-66.

646   Follows MJ, Dutkiewicz S, Grant S, Chisholm SW (2007) Emergent biogeography of microbial

647   communities in a model ocean. *Science,* **315**, 1843-1846.

648   Fraile I, Schulz M, Mulitza S, Kucera M (2008) Predicting the global distribution of planktonic

649   foraminifera using a dynamic ecosystem model. *Biogeosciences,* **5**, 891-911.

650   Gangsto R, Joos F, Gehlen M (2011) Sensitivity of pelagic calcification to ocean acidification.

651   *Biogeosciences,* **8**, 433-458.

652   Gehlen M, Bopp L, Ernprin N, Aumont O, Heinze C, Raguencau O (2006) Reconciling surface ocean

653   productivity, export fluxes and sediment composition in a global biogeochemical ocean

654   model. *Biogeosciences,* **3**, 521-537.

655   Hayes A, Kucera M, Kallel N, Sbaffi L, Rohling EJ (2005) Glacial Mediterranean sea surface

656   temperatures based on planktonic foraminiferal assemblages. *Quaternary Science Reviews,*

657   **24**, 999-1016.

658   Hemleben C, Spindler M, Anderson OR (1989) *Modern Planktonic Foraminifera,* New York, Springer-

659   Verlag.

660   Honjo, S (1996). Fluxes of particles to the interior of the open oceans. in Particle Flux in the Ocean,

661   Ittekkot, V, Schafer, P, Honjo, S, Depetris, PJ, Wiley, New York, 91–154.

662   Hourdin F, Musat I, Bony S *et al.* (2006) The LMDZ4 general circulation model: climate performance

663   and sensitivity to parametrized physics with emphasis on tropical convection. *Climate*

664   *Dynamics,* **27**, 787-813.

665   Jackson JBC, Sheldon PR (1994) Constancy and change of life in the sea. *Philosophical*

666   *Transactions of the Royal Society of London Series B-Biological Sciences,* **344**, 55-60.

667   Kageyama M, Braconnot P, Bopp L *et al.* (2012) Mid-Holocene and last glacial maximum climate

668   simulations with the IPSL model: part II: model-data comparisons. *Climate Dynamics*.

669   Keul N, Langer G., de Nooijer L. J., and Bijma, J. (2013) Effect of ocean acidification on the benthic

670   foraminifera Ammonia sp. is caused by a decrease in carbonate ion

671   concentration. *Biogeosciences*, *10*(10), 6185-6198.Key RM, Kozyr A, Sabine CL *et al.* (2004)

672   A global ocean carbon climatology: Results from Global Data Analysis Project (GLODAP).

673   *Global Biogeochemical Cycles,* **18**.

674   Kohfeld KE, Fairbanks RG, Smith SL, Walsh ID (1996) Neogloboquadrina pachyderma (sinistral

675   coiling) as paleoceanographic tracers in polar oceans: Evidence from northeast water

676   Polynya plankton tows, sediment traps, and surface sediments. *Paleoceanography,* **11**, 679-

677   699.

678   Krinner G, Viovy N, de Noblet-Ducoudre N *et al.* (2005) A dynamic global vegetation model for studies

679   of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles,* **19**.

680   Kucera M, Weinelt M, Kiefer T *et al.* (2004) Compilation of planktic foraminifera census data, modern

681   from the Atlantic Ocean. PANGAEA, doi:10.1594/PANGAEA.227322.

682   Kucera M, Rosell-Mele A, Schneider R, Waelbroeck C, Weinelt M (2005) Multiproxy approach for the

683   reconstruction of the glacial ocean surface (MARGO). *Quaternary Science Reviews,* **24**, 813-

684   819.

685   Kuroyanagi A, Kawahata H (2004) Vertical distribution of living planktonic foraminifera in the seas

686   around Japan. *Marine Micropaleontology,* **53**, 173-196.

687   Langer, G, Nehrke, G, Probert, I, Ly, J, and Ziveri, P. (2009) Strain-specific responses of *Emiliania*

688   *huxleyi* to changing seawater carbonate chemistry. Biogeosciences, **6**, 2637–2646.

689   Lombard F, da Rocha RE, Bijma J, Gattuso JP (2010) Effect of carbonate ion concentration and

690   irradiance on calcification in planktonic foraminifera. *Biogeosciences,* **7**, 247-255.

691   Lombard, F., Labeyrie, L., Michel, E., Spero, H. J., & Lea, D. W. (2009a). Modelling the temperature

692   dependent growth rates of planktic foraminifera.*Marine Micropaleontology*, *70*(1), 1-7.

693   Lombard F, Erez J, Michel E, Labeyrie L (2009b) Temperature effect on respiration and

694   photosynthesis of the symbiont-bearing planktonic foraminifera Globigerinoides ruber,

695   Orbulina universa, and Globigerinella siphonifera. *Limnology And Oceanography,* **54**, 210-

696   218.

697   Lombard F, Labeyrie L, Michel E *et al.* (2011) Modelling planktic foraminifer growth and distribution

698   using an ecophysiological multi-species approach. *Biogeosciences, 8*, 853-873.

699   Madec G, Delecluse P, Imbard M, Lévy M (1998) *OPA 8.1 Ocean General Circulation Model*

700   *Reference Manual. Notes du Pôle de Modélisation 11,* Paris, France, IPSL.

701   Manno C, Morata N, Bellerby R (2012) Effect of ocean acidification and temperature increase on the

702   planktonic foraminifer Neogloboquadrina pachyderma (sinistral). *Polar Biology, 35*, 1311-

703   1319.

704   Marland, G., and T. B. R. J. Andres (2005) Global, regional, and national CO_2 emissions. Trends: A

705   Compendium of Data on Global Change, Information Analysis Center, Oak Ridge National

706   Laboratory, U.S. Department of Energy.

707   McQuatters-Gollop A, Burkill PH, Beaugrand G, Johns DG, J.-P G, Edwards M (2010) *Atlas of*

708   *Calcifying Plankton: Results from the North Atlantic Continuous Plankton Recorder survey,*

709   Plymouth, UK, Sir Alister Hardy Foundation for Ocean Science.

710   Moy AD, Howard WR, Bray SG, Trull TW (2009) Reduced calcification in modern Southern Ocean

711   planktonic foraminifera. *Nature Geoscience, 2*, 276-280.

712   Nakicenovic, N., and Coauthors (2000) *IPCC Special Report on Emission Scenarios.* Cambridge

713   University Press.

714   Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan A, Gruber N,

715   Ishida A, Joos F, Key R. M., Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A,

716   Najjar RG, Plattner G, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD,

717   Totterdell IJ, Weirig M, Yamanaka Y,& Yool, A. (2005) Anthropogenic ocean acidification over

718   the twenty-first century and its impact on calcifying organisms. *Nature, 437*(7059), 681-686.

719   Ortiz JD, Mix AC, Collier RW (1995) Environmental-control of living symbiotic and asymbiotic

720   foraminifera of the California current. *Paleoceanography, 10*, 987-1009.

721   Pereira HM, Leadley PW, Proenca V *et al.* (2010) Scenarios for Global Biodiversity in the 21st

722   Century. *Science, 330*, 1496-1501.

723   Pinsonneault AJ, Matthews HD, Galbraith ED, Schmittner A (2012) Calcium carbonate production

724   response to future ocean warming and acidification. *Biogeosciences, 9*, 2351-2364.

725   Retailleau S, Schiebel R, Howa H (2011) Population dynamics of living planktic foraminifers in the

726   hemipelagic southeastern Bay of Biscay. *Marine Micropaleontology, 80*, 89-100.

727   Ridgwell A, Schmidt DN, Turley C, Brownlee C, Maldonado MT, Tortell P, Young JR (2009) From

728   laboratory manipulations to Earth system models: scaling calcification impacts of ocean

729   acidification. *Biogeosciences,* **6**, 2611-2623.

730   Ridgwell A, Zondervan I, Hargreaves JC, Bijma J, Lenton TM (2007) Assessing the potential long-

731   term increase of oceanic fossil fuel CO_2 uptake due to CO_2-calcification feedback.

732   *Biogeosciences,* **4**, 481-492.

733   Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FMM (2000) Reduced calcification of

734   marine plankton in response to increased atmospheric CO_2. *Nature,* **407**, 364-367.

735   Roy, T., Bopp, L., Gehlen, M., Schneider, B., Cadule, P., Frölicher, T. L., Segschneider J., Tjiputra J.,

736   Heinze C. & Joos, F. (2011). Regional Impacts of Climate Change and Atmospheric CO2 on

737   Future Ocean Carbon Uptake: A Multimodel Linear Feedback Analysis. *Journal of*

738   *climate*, *24*(9), 2300-2318.

739   Russell AD, Honisch B, Spero HJ, Lea DW (2004) Effects of seawater carbonate ion concentration

740   and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera. *Geochimica Et*

741   *Cosmochimica Acta,* **68**, 4347-4361.

742   Rutherford S, D'Hondt S, Prell W (1999) Environmental controls on the geographic distribution of

743   zooplankton diversity. *Nature,* **400**, 749-753.

744   Sarmiento JL, Slater R, Barber R *et al.* (2004) Response of ocean ecosystems to climate warming.

745   *Global Biogeochemical Cycles,* **18**.

746   Sautter LR, Thunell RC (1991) Planktonic foraminiferal response to upwelling and seasonal

747   hydrographic conditions - sediment trap results from San-Pedro-basin, southern California

748   bight. *Journal of Foraminiferal Research,* **21**, 347-363.

749   Schiebel R (2002) Planktic foraminiferal sedimentation and the marine calcite budget. *Global*

750   *Biogeochemical Cycles,* **16**.

751   Schiebel R, Movellan A (2012) First-order estimate of the planktic foraminifer biomass in the modern

752   global oceans. *Earth System Science Data Discussions,* **5**, 243-280.

753   Schiebel R, Waniek J, Bork M, Hemleben C (2001) Planktic foraminiferal production stimulated by

754   chlorophyll redistribution and entrainment of nutrients. *Deep-Sea Research Part I-*

755   *Oceanographic Research Papers,* **48**, 721-740.

756 Schiebel R, Zeltner A, Treppke UF, Waniek JJ, Bollmann J, Rixen T, Hemleben C (2004) Distribution

757   of diatoms, coccolithophores and planktic foraminifers along atrophic gradient during SW

758   monsoon in the Arabian Sea. *Marine Micropaleontology,* **51**, 345-371.

759 Schmittner A, Oschlies A, Matthews HD, Galbraith ED (2008) Future changes in climate, ocean

760   circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO_2

761   emission scenario until year 4000 AD. *Global Biogeochemical Cycles,* **22**.

762 Schneider B, Bopp L, Gehlen M *et al.* (2008) Climate-induced interannual variability of marine primary

763   and export production in three global coupled climate carbon cycle models. *Biogeosciences,*

764   **5**, 597-614.

765 Seferian R, Bopp L, Gehlen M *et al.* (2013) Skill assessment of three earth system models with

766   common marine biogeochemistry. *Climate Dynamics,* **40**, 2549-2573.

767 Siegel DA, Deuser WG (1997) Trajectories of sinking particles in the Sargasso Sea: modeling of

768   statistical funnels above deep-ocean sediment traps. *Deep-Sea Research Part I-*

769   *Oceanographic Research Papers,* **44**, 1519-1541.

770 Spero HJ (1992) Do planktic foraminifera accurately record shifts in the carbon isotopic composition

771   of seawater sigma-CO_2. *Marine Micropaleontology,* **19**, 275-285.

772 Spero HJ, Bijma J, Lea DW, Bemis BE (1997) Effect of seawater carbonate concentration on

773   foraminiferal carbon and oxygen isotopes. *Nature,* **390**, 497-500.

774 Spero HJ, Lea DW (1993) Intraspecific stable-isotope variability in the planktic foraminifera

775   *globigerinoides-sacculifer* - results from laboratory experiments. *Marine Micropaleontology,*

776   **22**, 221-234.

777 Spindler M, Hemleben C, Salomons JB, Smit LP (1984) Feeding-behavior of some planktonic

778   foraminifers in laboratory cultures. *Journal of Foraminiferal Research,* **14**, 1-3.

779 Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., ... & Segschneider, J.

780   (2010). Projected 21st century decrease in marine productivity: a multi-model analysis.

781   *Biogeosciences*, **7**(3), 979-1005.

782 von Gyldenfeldt AB, Fahrbach E, Garcia MA, Schroder M (2002) Flow variability at the tip of the

783   Antarctic Peninsula. *Deep-Sea Research Part Ii-Topical Studies In Oceanography,* **49**, 4743-

784   4766.

785 Watkins JM, Mix AC, Wilson J (1996) Living planktic foraminifera: Tracers of circulation and

786   productivity regimes in the central equatorial Pacific. *Deep-Sea Research Part Ii-Topical*

787   *Studies In Oceanography,* **43**, 1257-1282.

788 Watkins JM, Mix AC, Wilson J (1998) Living planktic foraminifera in the central tropical Pacific Ocean:

789   articulating the equatorial 'cold tongue' during La Nina, 1992. *Marine Micropaleontology,* **33**,

790   157-174.

791 Zaric S, Donner B, Fischer G, Mulitza S, Wefer G (2005) Sensitivity of planktic foraminifera to sea

792   surface temperature and export production as derived from sediment trap data. *Marine*

793   *Micropaleontology,* **55**, 75-105.

794 Zondervan I, Zeebe RE, Rost B, Riebesell U (2001) Decreasing marine biogenic calcification: A

795   negative feedback on rising atmospheric pCO(2). *Global Biogeochemical Cycles,* **15**, 507-

796   516.

797

798

6. Tables

Table 1. Key species-specific parameters used in the FORAMCLIM model. The half saturation constant for the Michaelis-Menten relationship that describes the influence of food availability on the nutrition rate, k_n; the fraction of the symbiont photosynthesis that is utilized in foraminiferal growth, $^{\%}p$; and the number of symbionts per individual 250 μm foraminifer, s_{nb}.

	k_n (μgC L^{-1})	$^{\%}p$	s_{nb}
O. universa	1.73	0.46	716
G. sacculifer	1.32	0.40	1160
G. siphonifera	1.19	0.30	720
G. ruber	0.51	0.37	1104
N. dutertrei	1.00	-	-
G. bulloides	6.84	-	-
N. incompta	3.33	-	-
N. pachyderma	4.70	-	-

Table 2. Assessment of the simulated distribution of foraminiferal species (percentage of area with model-data agreement) using the plankton tow data of Bé and Tolderlund (1971). The RMSE of diversity and relative abundance are assessed against the MARGO top-core data. *Lombard[1]* is the model-based (FORAMCLIM) estimate from Lombard *et al.* (2010); *Lombard[2]* refers to the satellite-based estimate from Lombard *et al.* (2010); *Fraile[1]* refers to the model-based (PLAFOM) estimate from Fraile *et al.* (2008).

	This study	Other studies		
		Lombard[1]	*Lombard[2]*	*Fraile[1]*
Dominant species (%)	43%	59%	71%	
Diversity (RMSE)	0.56	0.48	0.52	
Relative abundance (RMSE)				
O. universa	3.2	3.24	3.28	-
G.sacculifer	12.1	12.38	17.46	23
G. siphonifera	6.1	5.29	6.00	-
G. ruber	24.1	23.14	17.76	25
N. dutertrei	18.3	17.53	17.23	-
G. bulloides	22.0	21.02	18.97	25
N. incompta	16.2	15.85	14.85	22
N. pachyderma	20.6	17.01	12.32	9

7. Figures

Figure 1

Present (a,c) and future changes (b,d) in the total simulated abundance (all species). (a,c) column-integrated abundance (Ind m^{-2}), and (b, d) zonal-mean abundance (Ind m^{-3}).
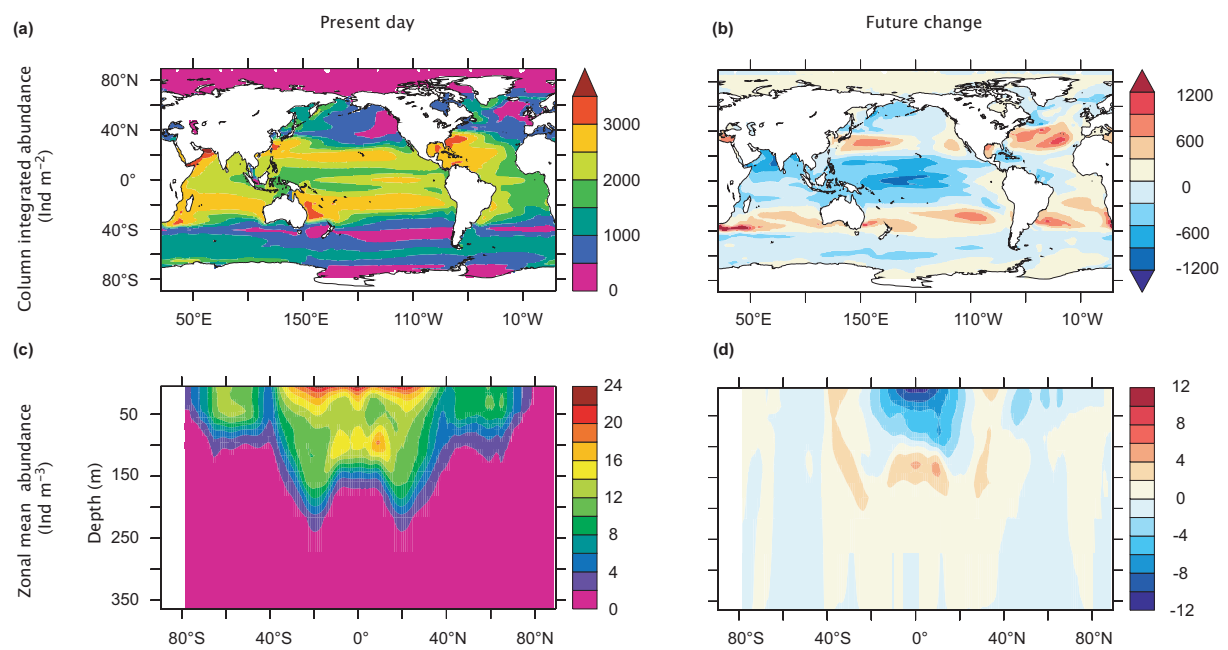
Figure 2

Total surface abundance of foraminifera (Ind m^{-3}): (a) present-day surface distribution, and (b) zonally-averaged surface abundance for the present-day and the future. Shannon diversity index of the simulated foraminifera: (c) surface distribution, and (d) zonally-averaged for the present-day and future.
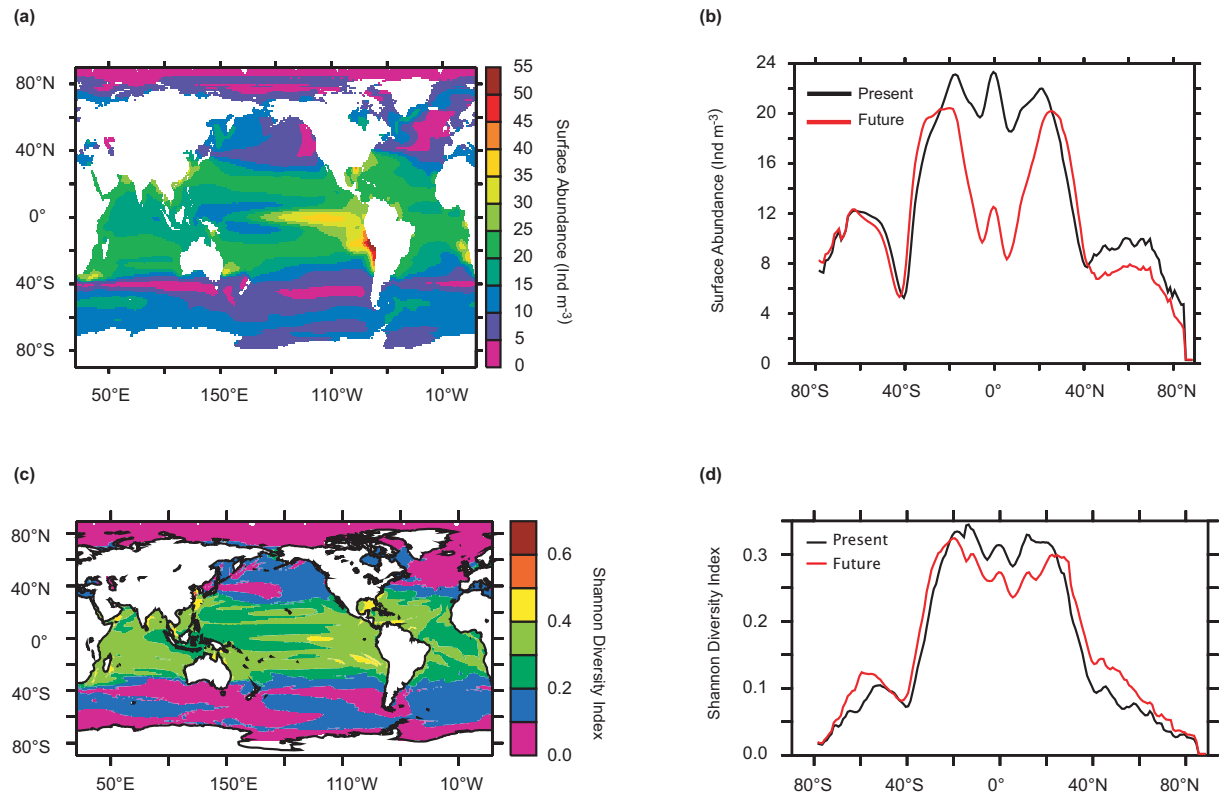
Figure 3

Zonally averaged changes (i.e. present – future) in the abundance and the relative abundance of each foraminifer species simulated in FORAMCLIM at (a,c) the ocean surface, and (b, d) integrated throughout the water column.
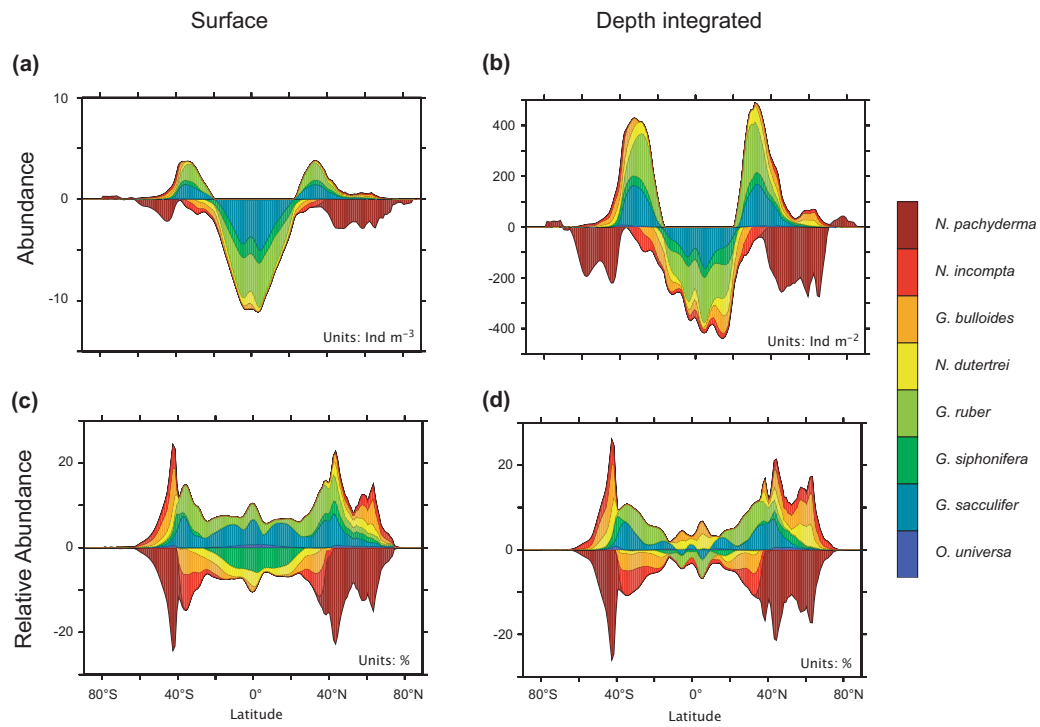
Figure 4

Future changes by 2100 in the dominant environmental drivers of foraminiferal abundance. Ocean temperature (°C): (a) at the surface and (b) zonally averaged. Phytoplankton concentration (μC L^{-1}): (c) at the surface, and (d) zonally averaged.
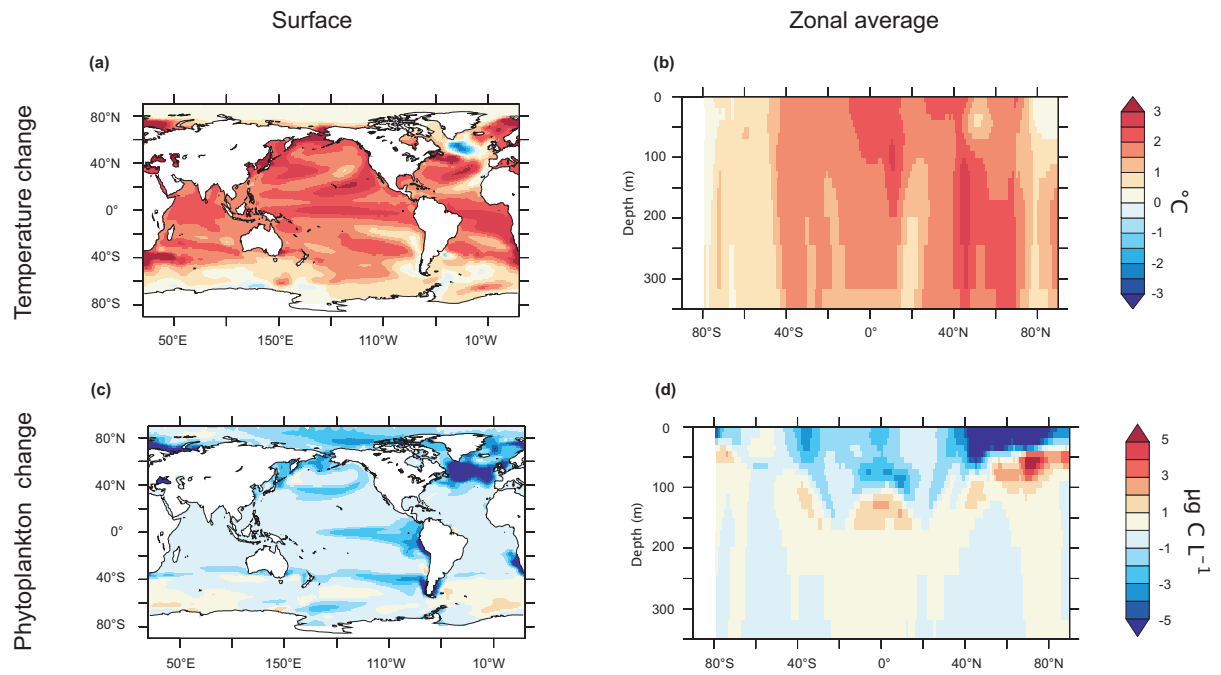
Figure 5

Components of the future change by 2100 in total foraminiferal abundance due to temperature: (a) depth integrated (Ind m^{-2}), (b) zonally-averaged (Ind m^{-3}). Components of the future change in total foraminiferal abundance due to food availability: (c) depth integrated (Ind m^{-2}), (d) zonally-averaged (Ind m^{-3}).
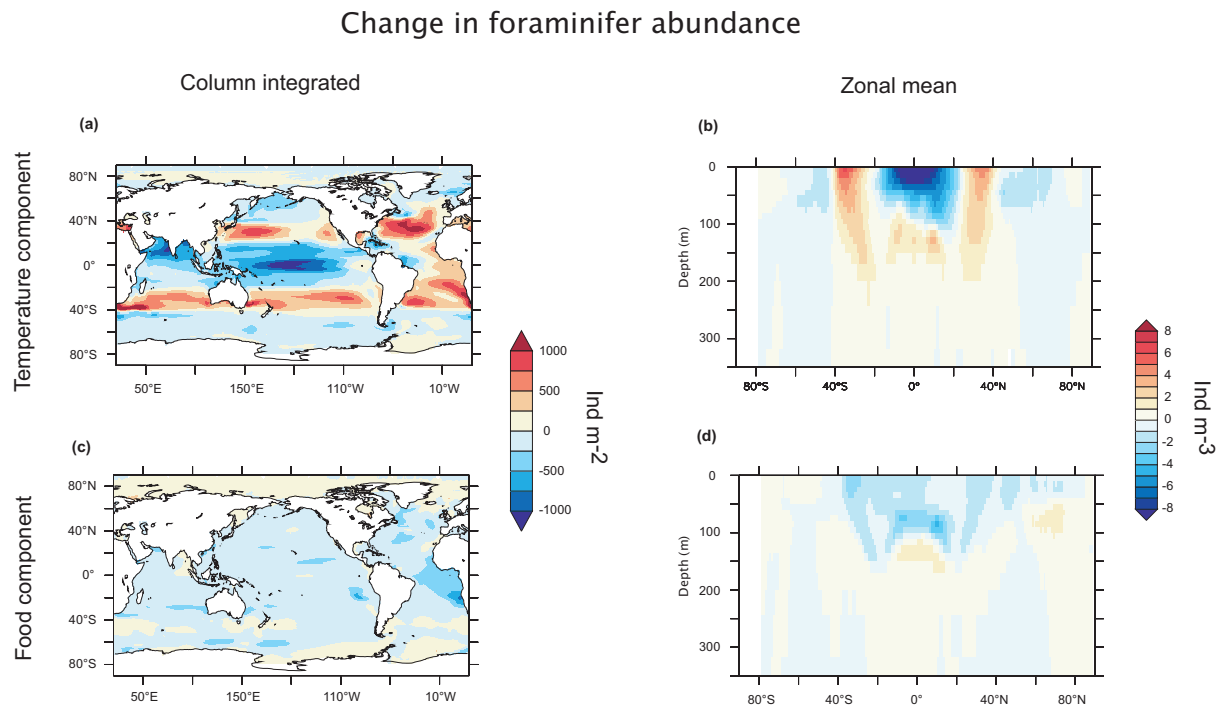
Figure 6

Future change (%) in the potential habitat range (blue) and abundance (red) of each foraminiferal species. Potential habitat range is defined as the area where a foraminifer has the potential to grow given the environmental conditions (i.e. temperature, food availability and light).
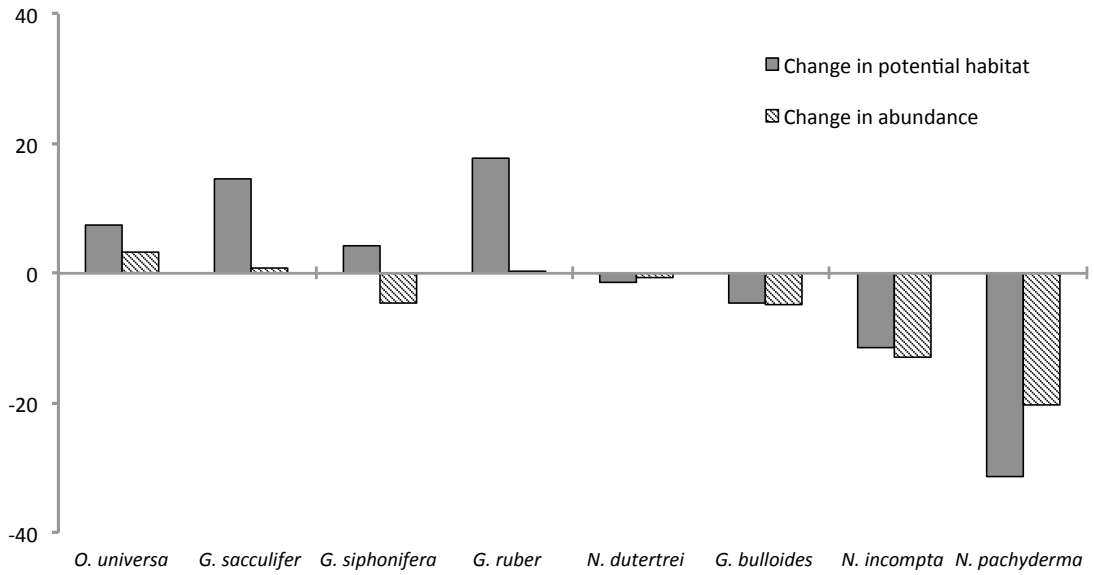
Figure 7

Percentage of the foraminiferal species abundance, collected with multinet plankton tows, that resides in each Ω_c class.
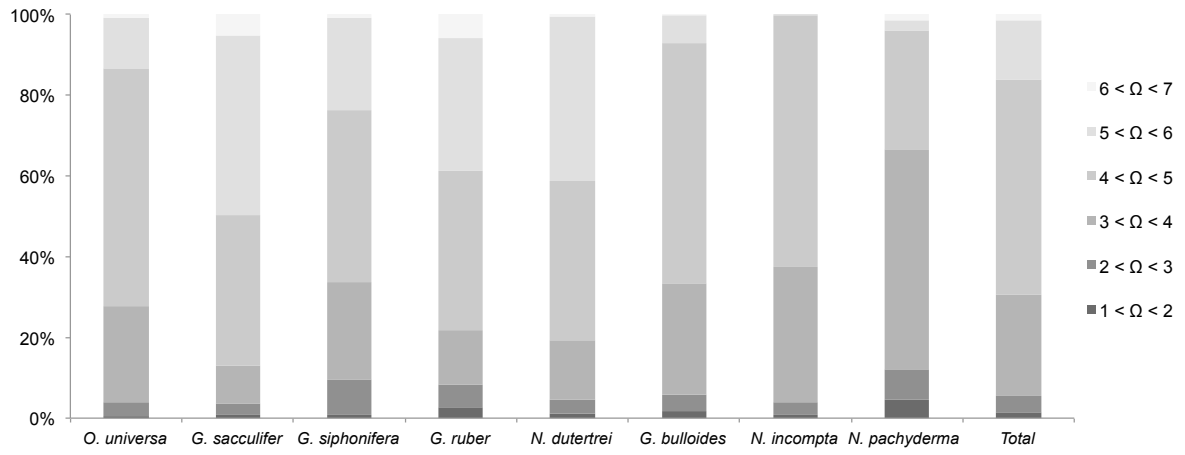
Figure 8

Future changes in carbon chemistry of the potential suitable habitat of foraminifera. Simulated present-day total abundance of foraminifera: (a) zonal mean (Ind m^{-3}), and (b) surface (Ind m^{-3}). Contours represent the calcite saturation state, Ω_C, for the present-day (black) and the future (pale blue). For each foraminifer species: (c) the percentage of the future potential habitat with low calcite saturation states, $\Omega_C < 2$, and (d) the simulated present and future carbonate ion concentration (μmol kg^{-1}) of the potential habitat.
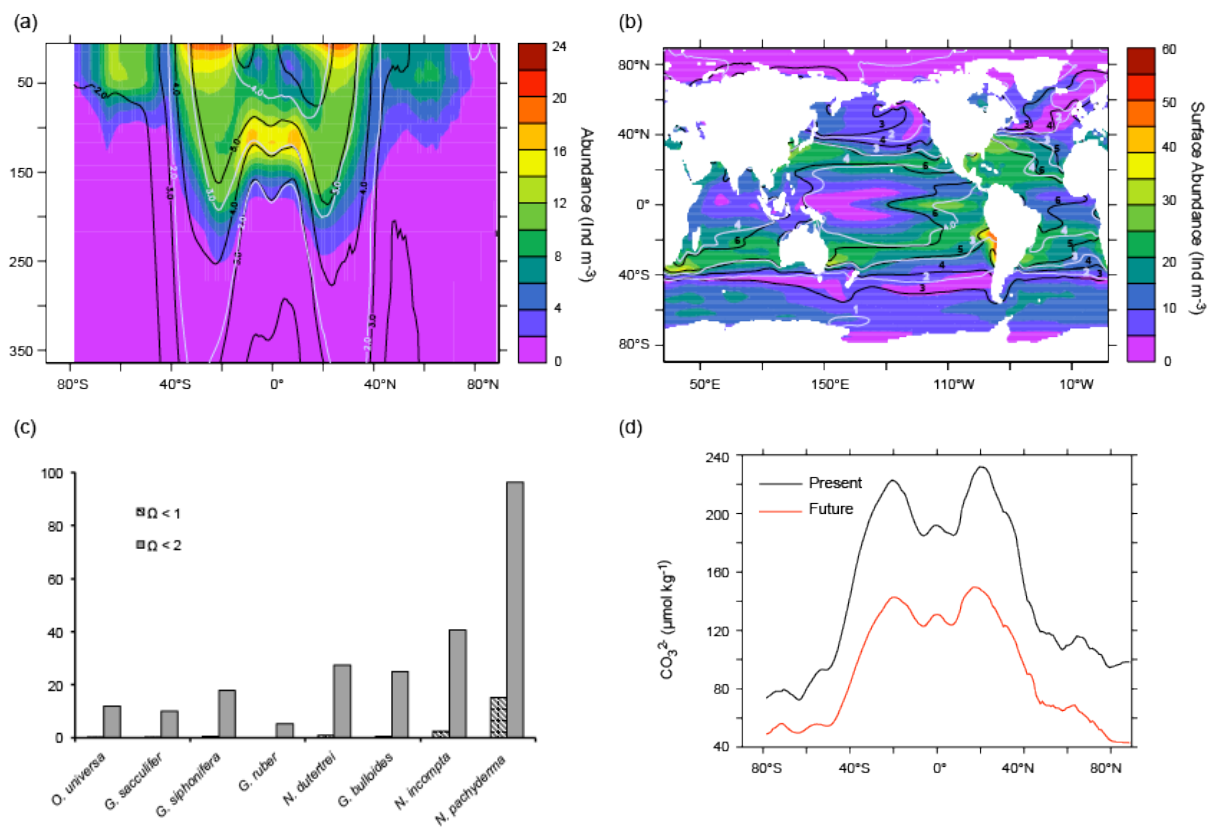
8. Supplementary material

Figure S1

Temperature dependence of the nutrition component of the growth rate (day^{-1}, see N(T,F) in Lombard *et al.*, 2009a) for the eight species included in the FORAMCLIM model.
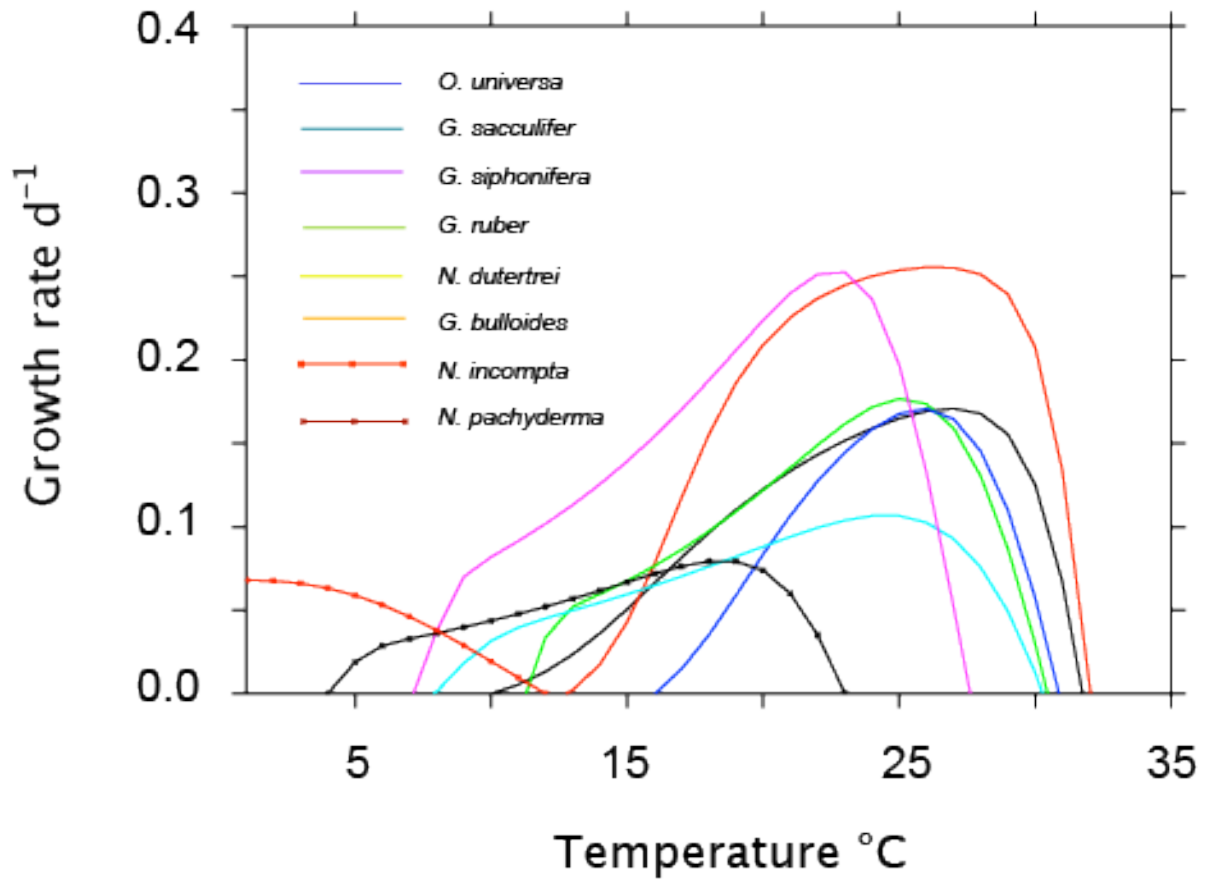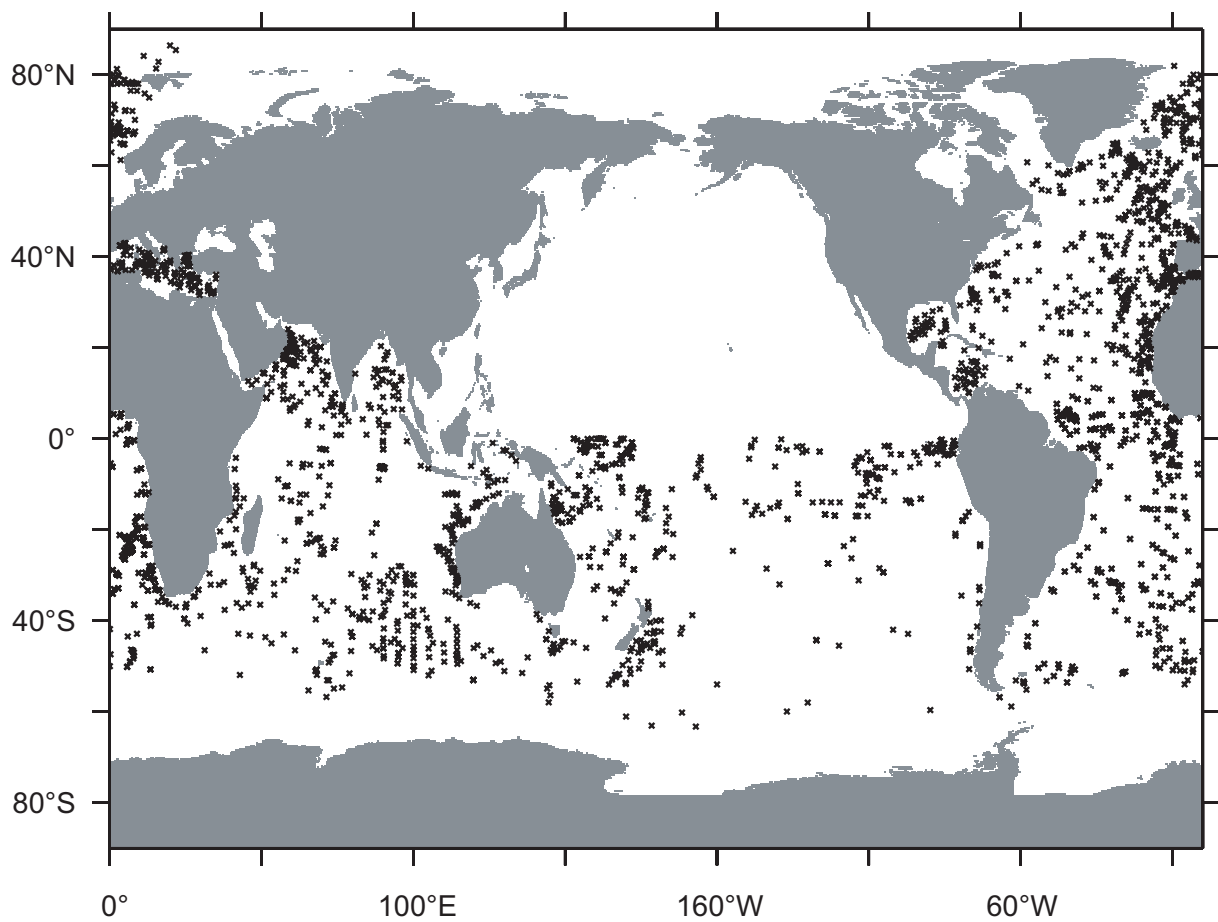
Figure S2

 (a) Locations of top-core sediment core data (MARGO database) used for model evaluation. (b) The calcite saturation state of the surface ocean from GLODAP (Key *et al.,* 2004). Red crosses are the locations of multinet plankton tows used to 'sample' the calcite saturation state of present-day foraminiferal habitat (Field, 2004; Kuroyanagi and Kawahata, 2004; Schiebel et al., 2001, 2004; Watkins et al., 1996, 1998).
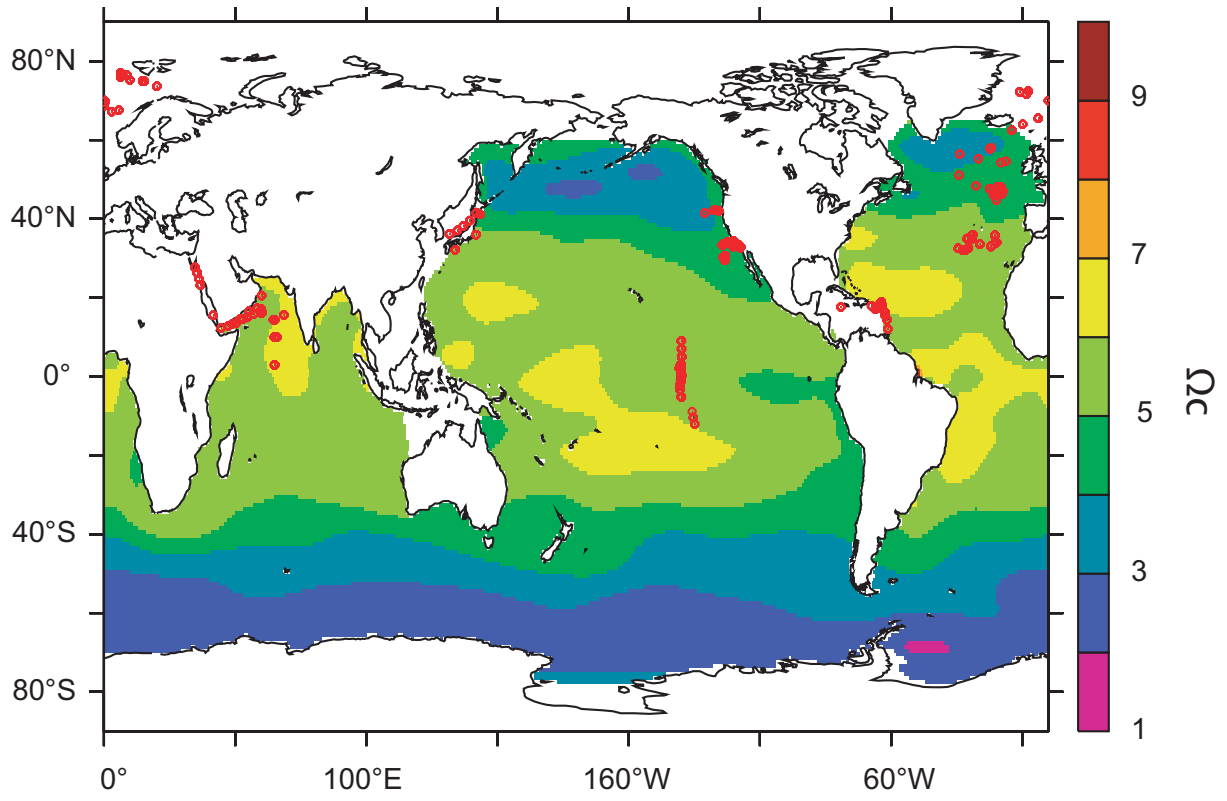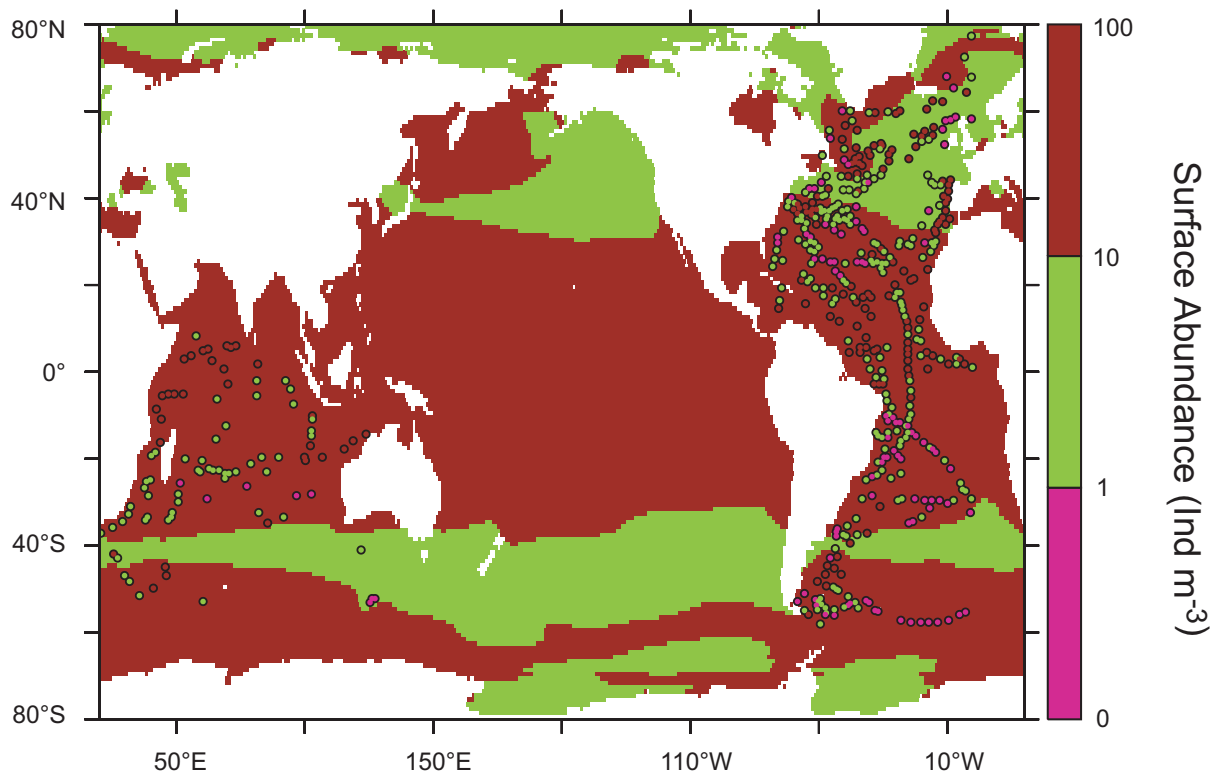
(a)

(b)

Figure S3

Present-day (simulated and observed) surface (a) total (all species) foraminiferal abundance (Ind m^{-3}), and (b) dominant foraminiferal species (i.e. the most abundant) based on the eight species included in the FORAMCLIM model. Circles represent the surface plankton tow data of Bé and Tolderlund (1971).

(a)

(b)

Legend:
- N. pachyderma
- N. incompta
- G. bulloides
- N. dutertrei
- G. ruber
- G. siphonifera
- G. sacculifer
- O. universa