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Future vulnerability of marine biodiversity compared with contemporary and past changes

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Many studies have implied significant effects of global climate change on marine life. Setting these alterations into the context of historical natural change has not been attempted so far, however. Here, using a theoretical framework, we estimate the sensitivity of marine pelagic biodiversity to temperature change and evaluate its past (mid-Pliocene and Last Glacial Maximum (LGM)), contemporaneous (1960–2013) and future (2081–2100; 4 scenarios of warming) vulnerability. Our biodiversity reconstructions were highly correlated to real data for several pelagic taxa for the contemporary and the past (LGM and mid-Pliocene) periods. Our results indicate that local species loss will be a prominent phenomenon of climate warming in permanently stratified regions, and that local species invasion will prevail in temperate and polar biomes under all climate change scenarios. Although a small amount of warming under the RCP2.6 scenario is expected to have a minor influence on marine pelagic biodiversity, moderate warming (RCP4.5) will increase by threefold the changes already observed over the past 50 years. Of most concern is that severe warming (RCP6.0 and 8.5) will affect marine pelagic biodiversity to a greater extent than temperature changes that took place between either the LGM or the mid-Pliocene and today, over an area of between 50 (RCP6.0: 46.9–52.4%) and 70% (RCP8.5: 69.4–73.4%) of the global ocean.

Many studies have suggested that climate influences local species abundance, community structure and biodiversity, phenology and species range in the marine environment[1–5]. To understand the magnitude of these changes, we need not only to understand the sensitivity of species and communities to temperature on a global scale, but also to give them a historical perspective. Here, to address this, we have first postulated that the arrangement of life in the oceans is the result of the interaction between the ecological niche and the regional environmental regime[6–10]. By implementing fundamental ecological principles (for example, Hutchinson's niche[11], Gause's principle of competitive exclusion[12]) into a theoretical model, we can create pseudo-communities for any given region of the global ocean[7]. Each pseudo-community results from the aggregation of pseudo-species, each characterized by a unique niche. By focusing exclusively on the thermal niche, it is possible to see how marine biodiversity and its organization in space and time are influenced by climate-induced changes in temperature[7–10] (Methods). We test our framework against observed data for foraminifers, crustaceans (copepods and euphausiids), fish (oceanic sharks and tuna/billfish) and cetaceans. This approach is different from previous analyses that applied ecological nichemodels[13,14] and also from more recent studies that examined isothermal changes[15,16]. These studies were limited at the community level by our poor understanding of the spatial distribution of many species[8], or due to a lack of biological knowledge, respectively. Having modelled the arrangement of life in the ocean, we then compare biodiversity vulnerability to past (LGM and mid-Pliocene) and contemporary (1960–2013) changes in temperature with future climate change scenarios (2081–2100) to set climate-induced changes in biodiversity into context.

Reconstruction of large-scale biodiversity patterns

To estimate biodiversity sensitivity, we used a framework based on the MacroEcological Theory on the Arrangement of Life[6–8] (Methods). This theory proposes that the arrangement of life results from the interaction between the ecological niche of species and changes in their environment[6–8,10,17]. A large number of pseudo-species can be generated, each having a unique ecological niche (here a one-dimensional thermal niche), and the interactions of the pseudo-species with the fluctuations in the local environmental regime (here the thermal regime) reconstruct the arrangement of biodiversity in space and time[7,8] (Methods). We therefore allowed pseudo-species to colonize any given region of the global ocean provided they could withstand the local annual sea surface temperature (SST). Locally, these pseudo-species collected into pseudo-communities. We found that the biodiversity resulting from this model based on annual SST values (Fig. 1a) was very similar to large-scale biodiversity patterns modelled previously[7] at a weekly temporal resolution using rectangular niches ($r = 0.99$; $p < 0.01$; $n = 9{,}927$, $n^* = 4$); this indicates that biodiversity patterns are unaffected significantly by either the absence or consideration of seasonality (annual versus weekly SST), or the niche shape (Gaussian versus rectangular). Correlations between expected and observed global biodiversity patterns for foraminifers were $r = 0.74$ ($p < 0.01$; $n = 1{,}040$, $n^* = 7$) and $r = 0.88$ ($p < 0.01$; $n = 8{,}649$, $n^* = 5$) using the Brown University Foraminiferal Data Base[18]

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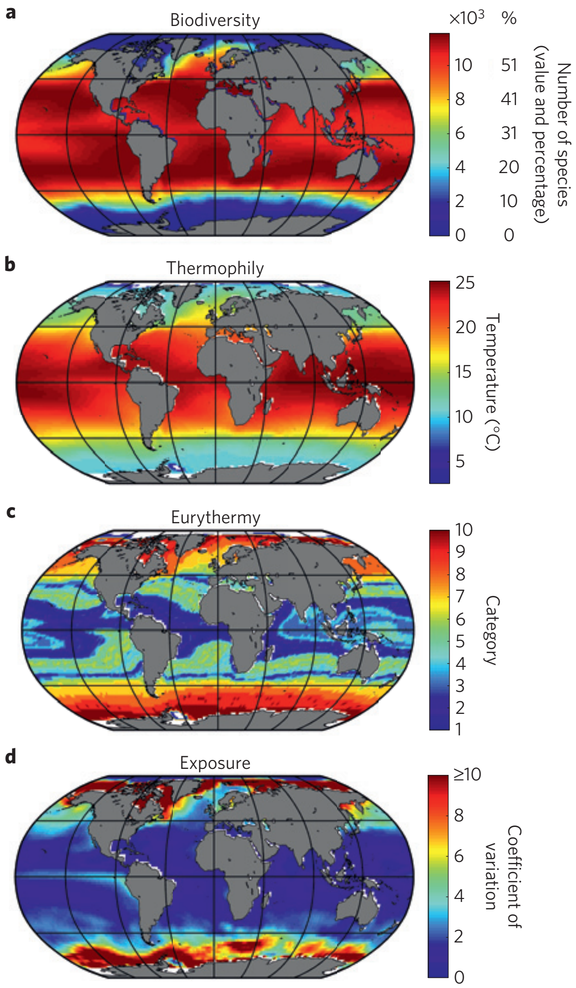

Figure 1 | Large-scale spatial patterns in some biodiversity and climatic properties. a–c, Biodiversity (pseudo-species richness; **a**), degree of thermophily (**b**) and eurythermy (**c**) of all pseudo-communities. **d**, Exposure as measured by the coefficient of variation of annual SST (1960–2013). 19,609 pseudo-species were created and biodiversity (**a**) is also represented as the percentage of created species. The degree of eurythermy is represented as category, with each category indicating a decile from 1 to 10.

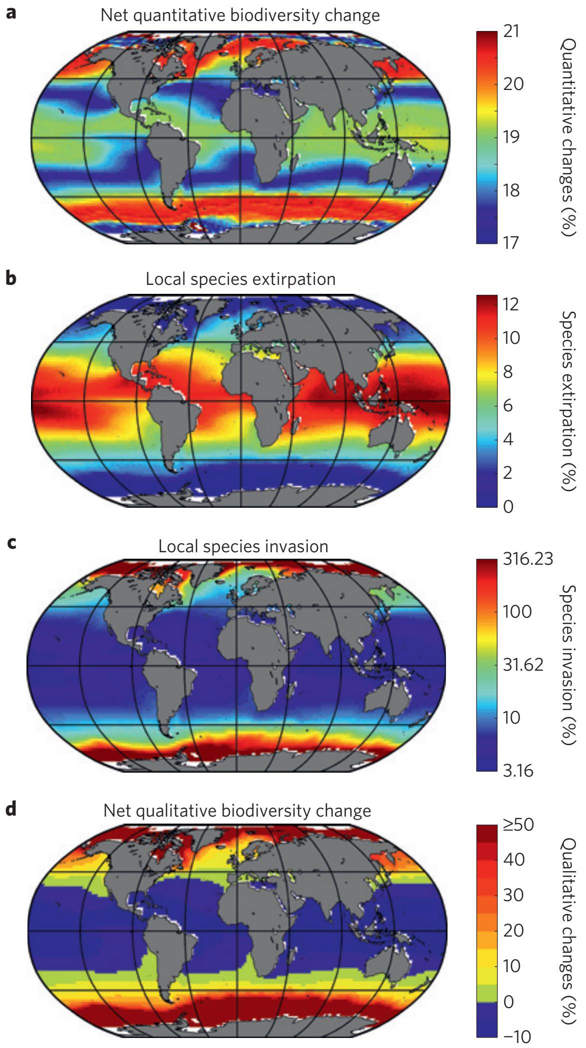

Figure 2 | Expected sensitivity of biodiversity to a 2 °C increase in temperature. a–c, Net quantitative changes in biodiversity (**a**), local species extirpation (**b**) and invasion (**c**). **d**, Net qualitative biodiversity changes resulting from the difference between species invasion and extirpation. All changes are expressed in percentage.

(Supplementary Fig. 1) or the gridded data of ref. 19, respectively. The same correlation was $r = 0.57$ ($p < 0.01$; $n = 433$, $n^* = 13$) for copepods; (Supplementary Fig. 1), $r = 0.76$ for euphausiids[19] ($p < 0.01$; $n = 8{,}644$, $n^* = 7$), $r = 0.77$ for oceanic sharks[19] ($p < 0.01$; $n = 7{,}961$, $n^* = 7$), $r = 0.76$ for tuna/billfish[19] ($p < 0.01$; $n = 8{,}182$, $n^* = 7$), and $r = 0.54$ for cetaceans[19] ($p < 0.01$; $n = 8{,}649$, $n^* = 13$). High-biodiversity regions coincided with areas where communities were composed of more thermophilic species and in those areas, biodiversity was maximum in regions where communities were more eurythermic (Fig. 1a–c). Biodiversity was high in areas where exposure, the magnitude of climate change in a given region (measured by changes in SST), was low (Fig. 1d). Low-biodiversity regions corresponded to areas where communities were more psychrophilic and exhibited a high degree of eurythermy, corresponding to areas where exposure was elevated (Fig. 1b–d).

Sensitivity of biodiversity to a 2 °C increase in temperature

We estimated biodiversity sensitivity to a uniform 2 °C increase in annual SST across the global ocean using different indices (Methods) and we investigated the theoretical sensitivity of biodiversity to temperature without the effect of exposure (that is, the local effect of climate change or variability on annual SST). In this way, local change results from the intrinsic property of the local community. The examination of quantitative biodiversity changes (that is, average of individual changes in expected species abundance) showed that polar communities are more sensitive to temperature; here, a 2 °C temperature rise brought about a change of ~20–21% in the average abundance of all pseudo-species (Fig. 2a). In contrast, subtropical communities are less sensitive to temperature (~17–18% of quantitative change), which may explain why more biodiversity is concentrated here[7] (Fig. 1a). Equatorial regions have a sensitivity intermediate between the poles and the tropics (~19%), which may indicate why biodiversity diminishes equatorwards (the well-known, hump-shaped biodiversity pattern[20]). The differences between quantitative biodiversity changes of the polar and the subtropical biomes were small (maximum difference of 4%, which may however represent a large quantitative difference at the community scale when many species are involved; Fig. 1a), suggesting that quantitative biodiversity changes may be more influenced by exposure (external component) than sensitivity (intrinsic component).

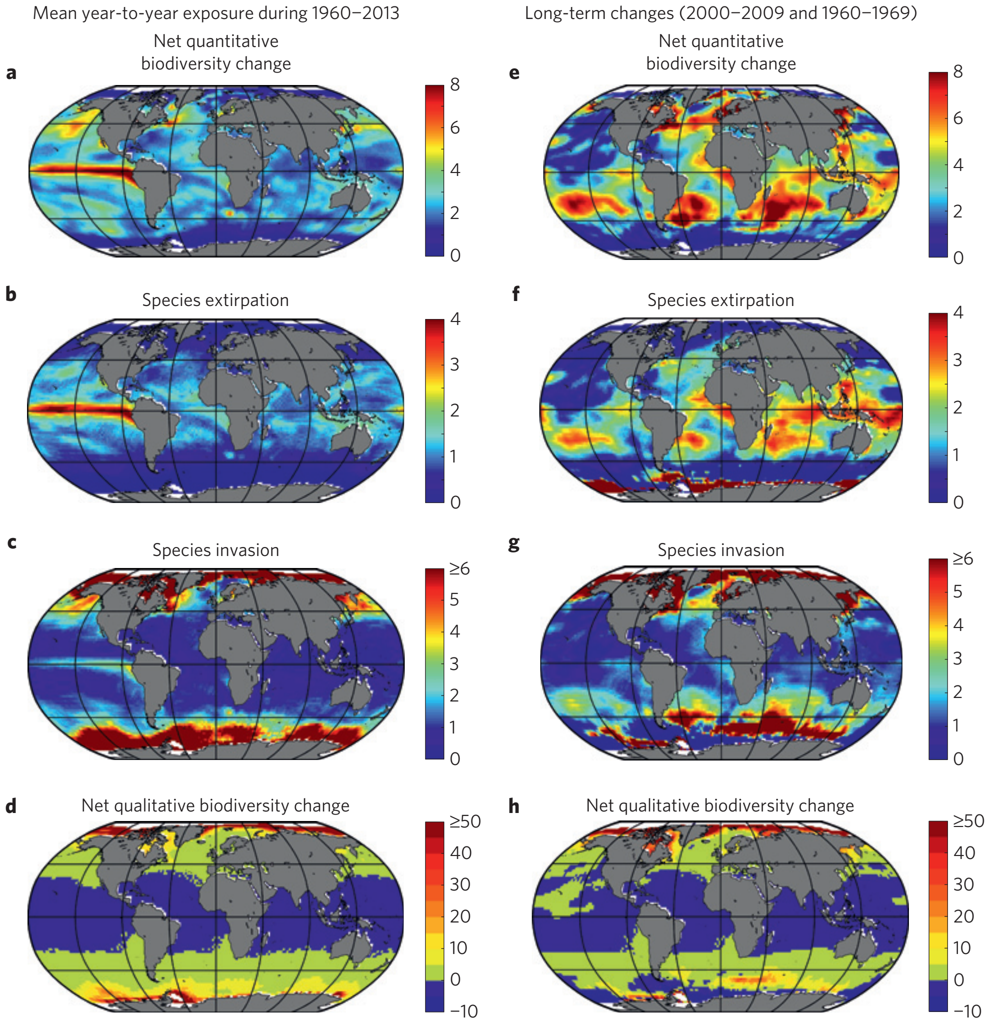

Figure 3 | Expected vulnerability of biodiversity to changes in annual SST. a–d, Expected vulnerability of biodiversity to average year-to-year changes in annual SST (1960–2013). **e–h**, Expected vulnerability of biodiversity to changes in annual SST between 2000–2009 and 1960–1969. Net quantitative changes in biodiversity (**a**,**e**), local species extirpation (**b**,**f**) and invasion (**c**,**g**) are shown. **d**,**h**, Net qualitative biodiversity changes that result from the difference between species invasion and extirpation. All changes are expressed in percentage.

Qualitative changes were also examined (Methods). Local species extirpation (that is, local species loss) was high in tropical systems for a 2 °C increase in annual SST and remained noticeable in extratropical regions, although it was more modest polewards (Fig. 2b). Examination of local species invasion revealed that biodiversity could increase substantially outside permanently stratified areas, especially in polar biomes; we saw up to 310% of increase in pseudo-species richness for a 2 °C increase in annual SST (Fig. 2c). This agrees with the reported high vulnerability of polar ecosystems to climate change[21]. In temperate biomes, the increase in pseudo-species richness ranged from 10 to 50%. Resulting, net qualitative biodiversity changes (that is, difference between local invasion and extirpation normalized by initial species richness) showed that biodiversity increased polewards with a reduction in permanently stratified regions (Fig. 2d). In contrast to quantitative changes, qualitative biodiversity changes were highly influenced by sensitivity (intrinsic component of the community).

Vulnerability of biodiversity to recent climate change

We assessed biodiversity vulnerability to temperature changes by combining sensitivity with exposure (Methods; Fig. 3). First, we assessed vulnerability to mean year-to-year variability in annual SST for 1960–2013. Only 5.3% of oceanic areas had important (that is, above 5%) quantitative community changes (Fig. 3a and Supplementary Table 1). Mean year-to-year vulnerability was strongest over the Pacific Ocean owing to the El Niño/Southern[22] and Pacific Decadal[23] oscillations. Vulnerability was also substantial in the western part of the North Atlantic Ocean and in the North Sea, where it may be affected by the North Atlantic Oscillation[24]. The analysis showed that a total of 14.1% of the global ocean experienced important species turnover (that is, the sum of species invasion and extirpation per geographical cell standardized by initial pseudo-species richness; Supplementary Table 1). There was no important local extirpation across the global ocean, although species local extirpation was elevated in the equatorial part of the Pacific Ocean (Fig. 3b). A total of 18.8% of the global ocean saw important local species invasion, particularly elevated in the polar biomes (Fig. 3c). The resulting net qualitative biodiversity changes showed an increase in biodiversity polewards and a reduction over permanently stratified areas (Fig. 3d).

Next, we assessed vulnerability associated with temperature changes between 2000–2009 and 1960–1969 (Fig. 3e–h). A total of 28.7% of the global ocean showed important net quantitative biodiversity changes that were located mainly in the Southern Hemisphere (western part of mid-latitude regions) and in the Northern

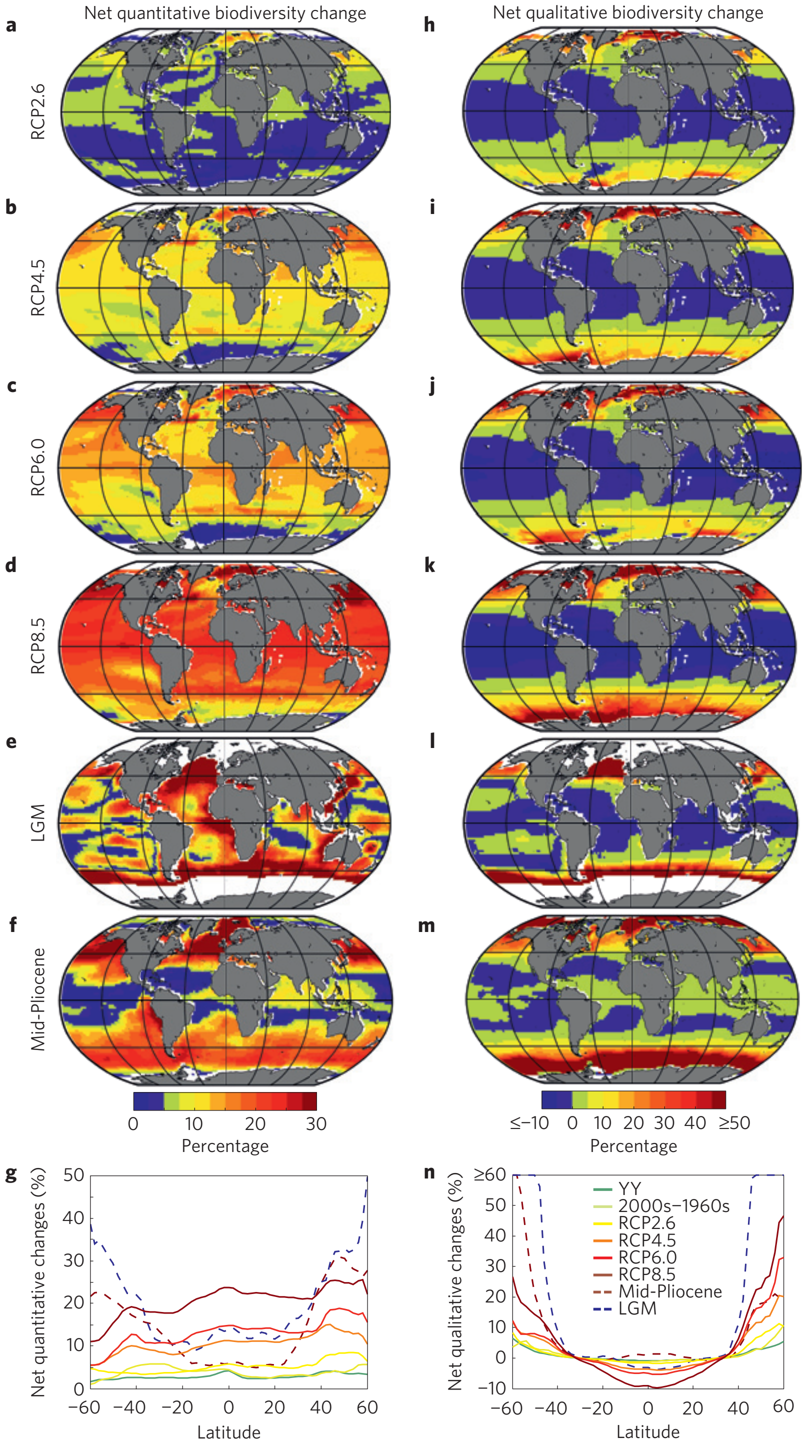

Figure 4 | Expected past and future mean vulnerability in biodiversity. a–f, Net quantitative biodiversity changes between 2081–2100 and 2006–2013 for scenarios RCP2.6 (**a**), RCP4.5 (**b**), RCP6.0 (**c**) and RCP8.5 (**d**), between the LGM and 1960–1969 (**e**) and 2006–2013 and thermal conditions corresponding to the mid-Pliocene (**f**). **h–m**, Net qualitative biodiversity changes for scenarios RCP2.6 (**h**), RCP4.5 (**i**), RCP6.0 (**j**) and RCP8.5 (**k**), between the LGM and 1960–1969 (**l**) and 2006–2013 and thermal conditions corresponding to the mid-Pliocene (**m**). **g**,**n**, Both net quantitative (**g**) and qualitative (**n**) changes were latitudinally averaged between 60° S and 60° N, including for comparison expected mean vulnerability changes in biodiversity corresponding to year-to-year variability (YY) in temperature (1960–2013; see Fig. 3a–d) and mean changes in temperature between 2000–2009 and 1960–1969 (Fig. 3e–h). All changes are expressed as percentage.

Hemisphere (along continents and in the North Atlantic temperate biome, including the North Sea; Fig. 3e and Supplementary Table 1). These changes agree with current observations of biodiversity changes in the northeast Atlantic and its adjacent seas over the same period[1,25]. Important species turnover and local extirpation concerned 21.6% and 2.6% of the global ocean, respectively. In the Southern Hemisphere, species local extirpation was high along the Equator and in the tropics (Fig. 3f). In the Northern Hemisphere, in contrast, species extirpation was less overall and restricted to regions south of the Polar Front (Fig. 3f and Supplementary Table 1).

Table 1 | Percentage of oceanic areas having net quantitative and qualitative (species turnover) biodiversity changes higher than those experienced between the LGM and the 1960s and between 2006–2013 and thermal conditions corresponding to the mid-Pliocene.

	LGM/1960–1969 ($276.6\ \mathrm{M\ km^2}$)		Mid-Pliocene/2006–2013 ($336.4\ \mathrm{M\ km^2}$)	
	Quantitative	Turnover	Quantitative	Turnover
Yearly	9.1% (24.8)	9.1% (24.8)	15.0% (49.8)	14.9% (49.7)
2000s–1960s	12.5% (34.1)	12.3 (33.6)	18.2% (60.2)	18.7% (61.7)
RCP2.6	15.5% (41.5)	15.3% (41.2)	25.3% (81.8)	25.4% (81.9)
RCP4.5	36.9% (99.1)	37.1% (99.7)	46.3% (149.4)	46.2% (148.9)
RCP6.0	46.9% (126.2)	47.6% (127.9)	51.2% (165.1)	52.4% (169.2)
RCP8.5	69.5% (186.7)	69.4% (186.5)	71.5% (230.6)	73.4% (236.8)

Yearly: biodiversity changes related to mean year-to-year variability in annual SST; 2000s–1960s: biodiversity changes related to changes in annual SST between 2000–2009 and 1960–1969; lines 3–6: biodiversity changes between annual SST between 2081–2100 and 2006–2013 for scenarios RCP2.6, RCP4.5, RCP6.0 and RCP8.5. Areas are expressed as percentage and as $\mathrm{km^2}$ in brackets.

Important species local invasion, found in 15.1% of oceanic areas, took place in polar biomes (Fig. 3g and Supplementary Table 1). The resulting net qualitative biodiversity showed a consistent increase in biodiversity polewards in both hemispheres and especially towards the North Pole (Fig. 3h). We tested the above results by comparing predicted changes in biodiversity to plankton data from the North Sea where sampling has occurred from 1960 onwards[26]. The predicted long-term changes in biodiversity were positively correlated to observed changes in North Sea copepod biodiversity (Supplementary Fig. 2; $r = 0.58$; $p_{\mathrm{ACF}} < 0.05$; $n = 50$). The predicted changes in biodiversity in the North Atlantic and its adjacent seas also match current observations for crustaceans and fish[27,28].

Vulnerability of biodiversity to future climate change

We assessed biodiversity changes associated with global warming using 4 Representative Concentration Pathway (RCP) scenarios and 5 different atmosphere–ocean general circulation models between 2081–2100 and the reference period 2006–2013 (Methods). We found that between $42.1 \pm 26.5\%$ (RCP2.6) and $94.4 \pm 9.8\%$ (RCP8.5) of the global oceans are likely to show important (that is, above 5%) net quantitative biodiversity changes (Supplementary Table 1); these changes appeared in the tropical and polar oceans and were especially pronounced in the Northern Hemisphere, although becoming quasi-global when the warming becomes severe (Fig. 4a–d). Important species turnover may concern between $33.2 \pm 20.4\%$ and $94.5 \pm 13.4\%$ of the global ocean (Supplementary Table 1). Between $16.5 \pm 6.9\%$ (RCP2.6) and $32.3 \pm 7.3\%$ (RCP8.5) of the global ocean is expected to exhibit an increase in biodiversity whereas between $6.3 \pm 4.8\%$ and $44 \pm 9.4\%$ (RCP8.5) of the global ocean is expected to reduce their local biodiversity (Fig. 4h–k and Supplementary Table 1). Although variations of these rates of biological change are substantial among atmosphere–ocean general circulation models, estimations become less variable when the intensity of the warming increases (Supplementary Table 1).

Net qualitative biodiversity changes were found to be negative (that is, more local extirpation than invasion) in permanently stratified regions and positive (that is, more local invasion than extirpation) in higher-latitude regions (for example, Nordic seas and the Southern Ocean; Fig. 4h–k). The loss in biodiversity becomes high for a pronounced warming (RCP6.0 and 8.5; Supplementary Table 1). The core of oceanic regions where local extirpation is predicted corresponds with source areas defined from climate velocities[16], corroborating the hypothesis that source areas may undergo loss of species richness[16]. Our theoretical predictions agree with projections based on 1,066 exploited species (fish and invertebrate), which revealed that net qualitative biodiversity changes are positive (more species local invasion than extirpation) towards high latitudes and negative (more local extirpation) in the tropics[13].

Vulnerability of biodiversity to past climate change

Large perturbations in temperatures took place between glacial and interglacial periods in the Quaternary and were responsible for major changes in the spatial distribution of many marine species[29,30]. It is therefore interesting to measure the extent to which future biodiversity changes may compare with natural changes that occurred between the LGM and today. Consequently, we assessed biodiversity changes between the LGM and the 1960s. During the LGM when CO_2 concentrations were around 190 ppm, global temperatures and mean sea level were 3–5 °C and 125 m lower than they were in the 1960s[31–33], respectively. Biodiversity reconstructions for the LGM were highly correlated with observed foraminifera LGM biodiversity[34] (Methods). For the three reconstructions (1–3), correlations ranged from $r = 0.92$ to $r = 0.93$ and were highly significant ($p < 0.01$): $r_1 = 0.93$ ($n_1 = 101, n_1{}^* = 5$), $r_2 = 0.92$ ($n_2 = 101$, $n_2{}^* = 5$) and $r_3 = 0.93$ ($n_3 = 93$, $n_3{}^* = 5$). Quantitative biodiversity changes observed between the LGM and the 1960s were substantial (>30%) in some extratropical regions and on the eastern margin of the Atlantic and Indian oceans, as well as the western part of the North Pacific Ocean (Fig. 4e). Local invasion took place in extratropical regions and local extirpation mainly occurred in the tropics (Fig. 4l). Important net quantitative biodiversity changes between the LGM and the 1960s concerned $84.6 \pm 0.9\%$ of the ocean. At that time important species turnover affected $77.9 \pm 2.4\%$ of the ocean and local species invasion was more important ($30.5 \pm 1.6\%$ of the ocean) than local extirpation ($22.5 \pm 1.7\%$; Supplementary Table 1).

The mid-Pliocene is also an interesting period because it is thought that global temperatures may be close to those predicted at present by the Intergovernmental Panel on Climate Change for the end of the century[35]. During the mid-Pliocene when CO_2 concentrations were ~400 ppm, global temperature and mean sea level were 2–3 °C and ~20 m higher than today, respectively[36–38]. Biodiversity reconstruction for the mid-Pliocene was correlated highly with observed foraminifera mid-Pliocene biodiversity[34] ($r = 0.67$, $p < 0.01, n = 242, n^* = 9$; Methods). We therefore calculated how a warming between 2006–2013 and a period corresponding to the mid-Pliocene would affect biodiversity and found that quantitative biodiversity changes would be high in extratropical regions (Fig. 4f). This could be because the mid-Pliocene was characterized by increased heat transport polewards, although it should be noted that the augmentation in the Atlantic meridional overturning circulation for this period has been recently challenged[39]. The current expectation for the end of the century is a slow-down in heat transport in the North Atlantic and Nordic seas related to a reduction in the Atlantic meridional overturning circulation[40]. Net qualitative biodiversity changes would be relatively low in permanently stratified regions, being slightly negative in mid-latitudes and positive in tropical regions (Fig. 4m). However, they would be relatively high outside permanently stratified areas, and especially in polar regions. Important net quantitative biodiversity changes between 2006–2013 and the mid-Pliocene would involve 74.6% of the global ocean, species turnover would affect 64.7%, and local species invasion would be much more important (37.8%) than local extirpation (1%; Supplementary Table 1).

Future, contemporary and past vulnerability in biodiversity

For scenario RCP2.6 the mean quantitative and qualitative biodiversity changes for the end of this century are similar to those observed as part of year-to-year natural variability in annual SST, or to those observed between the 2000s and the 1960s (Figs 3 and 4 and Supplementary Table 1). A similar result is found when global biodiversity changes (expressed as a percentage of the global ocean) are pooled as a function of intensity of biodiversity changes (Supplementary Fig. 3). When averaged latitudinally, biodiversity changes may be higher north of 40° N but remain low compared with changes that occurred between the LGM/mid-Pliocene and today (Fig. 4g,n). In scenario RCP2.6, 16% of the ocean is predicted to experience higher quantitative biodiversity change or species turnover than those experienced between the LGM and the 1960s (Table 1). Estimations are higher (~26%) when compared with the mid-Pliocene but remain low when compared with those induced by natural year-to-year variability in annual SST (~9% for LGM or ~15% for mid-Pliocene) or between the 2000s and the 1960s (~12% for LGM or ~18% for mid-Pliocene; Table 1).

For scenarios RCP4.5 to RCP8.5 (when warming becomes higher), the application of our model suggests that the marine biosphere may experience substantial changes in biodiversity. In scenario RCP4.5, important quantitative biodiversity changes occurred quasi-globally at the end of the century (Fig. 4b). We found that about 37% of the global ocean may experience greater changes in biodiversity (quantitative and qualitative) than those seen between the LGM/mid-Pliocene and today (Table 1). Such changes would be three times more frequent than and at least twice as intense as those experienced during the period 1960–2013 (~9–12% versus ~37% in Table 1 and Supplementary Fig. 3). During the period 1960–2013, major biological and ecological changes have already been observed, with strong potential implications on ecosystem functioning[2,4,41]. When averaged latitudinally, changes in biodiversity (quantitative and qualitative) are higher in the tropical ocean than those experienced between the LGM/mid-Pliocene and today (Fig. 4g,n). For a moderate warming (scenario RCP4.5), the rearrangement of the biodiversity should lead to an increase in the average local biodiversity in the global ocean as local invasion is higher than extirpation (Supplementary Table 1).

For scenarios RCP6.0 and 8.5 (severe warming), patterns of biodiversity change reach magnitudes similar to those experienced between the LGM/mid-Pliocene and today (Fig. 4). Changes in biodiversity will affect all permanently stratified regions and be strongest in the tropics. In the case of scenario 8.5, local extirpation in those regions may even be more pronounced than between the LGM/mid-Pliocene and today, and local invasion may become extensive in polar regions (Fig. 4). For scenarios RCP6.0 and RCP8.5, ~50% and ~70% of the global ocean is expected to witness biodiversity changes greater than those experienced between the LGM/mid-Pliocene and today, respectively (Table 1). In scenario RCP8.5, areas concerned by local extirpation become higher than areas concerned by local invasion, diminishing the average local biodiversity of the global ocean.

Potential limitations

Our study is based on two main assumptions. The first assumption is that the niche shape is constant over time and species rarely change biome (that is, niche conservatism)[42]. (Palaeoclimatologists use niche conservatism to reconstruct past climates and palaeoecologists use it to estimate species' past spatial distribution.) Of course, one way the niche shape may change over time to affect our predictions is through adaptation. We think this is unlikely for between now and the end of the present century however, because evolution is usually a slow process[43]. In contrast, slight changes in niche shape could have occurred for a few species between the LGM/mid-Pliocene and today owing to the greater length of time; although even here however, changes in niche shape are unlikely to have a large influence at the community scale because species rarely change biome even over tens of millions of years[42]. Second, we assume that temperature is the main driver of biodiversity; temperature is often the main environmental variable affecting biology used in studies such as ours[8,15,34] (Methods). Other environmental variables that would constitute the basis of a more complete analysis were unavailable for all time periods. Notwithstanding, we think that the benefit of using more ecological dimensions (for example, bathymetry, photosynthetically active radiation, chlorophyll or nutrients concentrations) would probably only be perceived at a regional/local scale, and that it is therefore unlikely to affect our conclusions, substantially. Other key ecological dimensions that also covary with temperature (for example, oxygen and macronutrients concentrations) at a global scale[44] can be considered implicitly in our analyses.

Conclusions

Our results show that climate change may rapidly reorganize marine biodiversity over large oceanic regions and that the intensity of this reorganization will depend, unsurprisingly, on the magnitude of warming. It should be noted that although climate change may increase biodiversity in extratropical regions, this will not compensate global species extinction related to direct anthropogenic forcing[45]. If global warming is small (RCP2.6), our study suggests that biological changes would reflect 15.5% of the amount of change seen between the LGM and the present day, or 25.3% of the amount of change observed between the mid-Pliocene and today; neither is that different from annual variability (1960–2013) and so it may therefore be benign overall. If warming is moderate (RCP4.5), changes in marine biodiversity will be three times more extensive and at least twice as strong in magnitude than changes observed over the past 50 years[41]. If global warming is severe (RCP6.0 and 8.5), between 50 and 70% of the global ocean will experience a change in biodiversity equivalent to, or higher than, that experienced between the LGM/mid-Pliocene and today indicating a major effect of climate warming on marine biodiversity. Any reorganization of marine biodiversity will inevitably affect interactions among species and consequently ecosystem functioning, provisioning and regulating services[13,28], highlighting the importance of understanding the effects of climate on biodiversity.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

G.B. conceived the study; G.B., V.R. and E.G. compiled the data; G.B. analysed the data. G.B., R.R.K., E.G., M.E. and V.R. discussed the results and wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to G.B. or R.R.K.

Competing financial interests

The authors declare no competing financial interests.

Methods

Annual sea surface temperatures. Annual sea surface temperatures (SSTs) originated from the data set ERSST_V3 (1960–2013). The data set is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set. Improved statistical methods have been applied to produce a stable monthly reconstruction, on a 1° × 1° spatial grid, based on sparse data[46].

We used outputs of SST from the latest generation of climate scenarios called RCPs (Representative Concentration Pathways)[47] to establish projections for the period 2081–2100. RCPs have replaced Special Report on Emissions Scenarios and provide a range of possible futures for the evolution of atmospheric composition[48]. We used SST outputs derived from five atmosphere–ocean general circulation models (AO-GCMs), listed in Supplementary Table 2. For each AO-GCM, we used the scenarios RCP2.6, RCP4.5, RCP6.0 and RCP8.5, which represent optimistic, intermediate and pessimistic outcomes. Scenario RCP6.0 was available in only three of the five AO-GCMs used in this study: IPSL-CM5A-MR, GISS-E2-H and HadGEM2-ES (Supplementary Table 2).

We used three different reconstructions of SST for the Last Glacial Maximum (LGM, ~20,000 years ago). The first data set was based on SST estimated from a transfer-function analysis of foraminiferal assemblages. Geometric patterns of surface waters were derived subsequently from water-mass-related assemblages of Coccolithophorida and Foraminifera[49]. We also used the two versions of gridded global SSTs provided in ref. 50; the 'line' version based on the LGM SST isolines and the 'core' version based on a kriging interpolation of SST data from deep-sea cores[51]. Data sets were downloaded from the National Climate Data Center (http://www.ncdc.noaa.gov).

Mean SSTs for the mid-Pliocene (mid-Piacenzian, 3.264–3.025 Ma) were produced by the Pliocene Research, Interpretation and Synoptic Mapping (PRISM) Group led by the US Geological Survey (http://www.usgs.gov). The latest PRISM reconstruction, PRISM3D, is based on multiple temperature proxies. Outputs of SST were modelled from faunal and floral assemblage data in the North Atlantic applying quantitative micropalaeontological methods[52]. The robustness of the data set was strengthened by using Mg/Ca values and alkenone unsaturation indices[53], and the spatial resolution was extended to the world[54].

Biological data. Contemporaneous biodiversity reconstructions were validated against large-scale observed biodiversity patterns of some pelagic groups: copepods (taxonomic richness), foraminifers (species richness), euphausiids, oceanic sharks, tuna/billfish and cetaceans. For copepod diversity, we used a previously compiled database of marine copepod species composition that extends over a latitudinal range from 86° N to 46° S that covers the Atlantic Ocean, and its adjacent seas, and North Pacific Ocean[20]. Taxonomic composition data were gridded (1° × 1° spatial resolution) and yearly taxonomic richness was calculated after pooling all samples within each grid cell. Yearly diversity values (taxonomic richness) were time-averaged over all observation years and log-transformed (decimal logarithm of richness). The resulting data matrix consisted of 433 geographical cells with copepod taxonomic richness data. Similarly, a comprehensive data set on the distribution of planktonic foraminiferal species (The Brown University Foraminiferal Data Base[18]) was used to calculate foraminiferal species richness in each grid cell. When several observations occurred in a spatial unit, average species richness was calculated. A total of 1,041 grid cells with log-transformed (decimal logarithm of richness) data on foraminiferal species richness were used. We also used the gridded data sets from ref. 19 on foraminifers, euphausiids, oceanic sharks, tuna/billfish and cetaceans. We did not use their data on pinnipeds because this taxonomic group shows a well-known inverse latitudinal biodiversity pattern, which is explained by the MacroEcological Theory on the Arrangement of Life (METAL) theory when biodiversity is decomposed into groups of different level of steno/eurythermy[7]. These gridded data are shown in figure 1 in ref. 19.

Past biodiversity reconstructions were tested using data sets of North Atlantic foraminifers for the LGM and the mid-Pliocene[34,55]. These data sets were composed of 32 LGM species from 101 sites and 44 mid-Pliocene species from 13 sites (242 samples).

Biological data of North Sea copepod biodiversity were taken from the Continuous Plankton Recorder (CPR) survey[26]. Species richness was calculated by summing all copepods in each CPR sample. Biodiversity for the period 1960–2009 was then spatially interpolated using the inverse squared distance method[56] in the region 56.5°–60.5° N and 0.5° W–6.5° E, corresponding to the northern part of the North Sea.

Overview of the METAL theory. The METAL theory states that biodiversity is influenced by climate and environment strongly and in a deterministic manner[6]. This influence mainly occurs through the interactions between the species ecological niche and both climatic, and environmental changes. The theory uses the concept of the ecological niche *sensu* Hutchinson (that is, the range of tolerance of a species when several factors are taken simultaneously) as an elementary emergent macroscopic process to predict at the species level local changes in abundance[17], species phenology and biogeographic range[8], phenological and biogeographical shifts[8], and at the community level the arrangement of biodiversity, including the latitudinal gradient in biodiversity[7], and long-term community/ecosystem shifts, including regime shifts[10]. We assume here that the ecological niche integrates the sum of many physiological processes occurring at both the individual and population levels. This theory offers a way to make testable ecological and biogeographical predictions to understand how life is organized, and how it responds to global environmental changes[6–8,10,17]. Pseudo-species and pseudo-communities can be generated throughout the ocean providing that their ecological niche enables them to withstand local changes in the climatic and the environmental regime in time. Actual communities represent only a subset of the theoretical pseudo-communities because not all niches are occupied in a given location[57]. A full description of the METAL theory and its limitations can be found in ref. 6.

Data selection. The ecological niche is multidimensional. Unfortunately, as recognized early[58], it is impossible to use all niche dimensions and so it is important to select a few that control a large part of the spatial distribution of species. The climate variability hypothesis states that the latitudinal range of species is primarily determined by their thermal tolerance[59]. In the marine realm, temperature is a key variable because it is the result of many hydro-climatic processes[60] and it exerts an effect on many fundamental biological and ecological processes[61]. The effects of temperature are especially strong for thermal-range conformers such as marine species (including invertebrates and fish) whose physiological thermal amplitude determines their latitudinal range at large spatial and temporal scales closely[61]. Phenological, biogeographical and long-term community shifts have also been correlated often to temperature[2,4,62,63]. Furthermore, the relationship between temperature and biodiversity is strong consistently for some marine species (for example, foraminifera) for the LGM and the mid-Pliocene[34], which are the two geologic periods investigated in this study.

Creation of pseudo-species. To reconstruct the global biodiversity pattern, we used a procedure similar to that in refs 7,8. We created pseudo-species, each having a unique Gaussian thermal niche with distinct degrees of eurythermy and thermophily[7,8]. All species were able to colonize a given region of the global ocean providing that they could withstand the local temperature (annual SST) regime. The response curve of the abundance E of a pseudo-species s in a given site i and time j to change in SSTs was modelled by the following function[64]:

$$E_{i,j,s} = c_s \mathrm{e}^{-((x_{i,j}-u_s)^2/2t_s^2)}$$

where $E_{i,j,s}$ is the expected abundance of a pseudo-species s at location i and time j; c_s is the maximum value of abundance for species s fixed to one; $x_{i,j}$ is the value of temperature at location i and time j; u_s is the thermal optimum and t_s is the thermal amplitude for species s. The thermal tolerance is an estimation of the breadth (or thermal amplitude) of the species thermal niche[64]. Once the niche was modelled, the expected abundance of such pseudo-species in space or time was determined from the knowledge of annual SST for a given year or time period and geographical cell. A large number of pseudo-species were created with u_s varying between −1.8 °C and 40 by 0.1 °C increments and t_s varying between 1.1 and 10 °C by increments of 0.05 °C. This represented a total of 39,218 potential species. However, to consider niche vacancy[7], we randomly selected half of this number. At the end of the procedure, only 19,609 species were used to model global oceanic biodiversity. Biodiversity was characterized by species richness (that is, the number of pseudo-species per geographical cell) and the degree of stenothermy/eurythermy (that is, weighted mean of the degree of stenothermy in each geographical cell) and thermophily/psychrophily of communities (that is, weighted mean of the degree of thermophily/psychrophily in each geographical cell; see Fig. 1a–c). We represented the degree of eurythermy using 10 categories, each representing a decile; for example, the first and last category corresponded to the first and last decile.

Terminology. Biodiversity vulnerability was here defined as the degree to which a community can be altered by climate-mediated changes in temperature[65]. It is the sum of all species' vulnerability, which in turn depends on sensitivity (intrinsic factor) and exposure (extrinsic factor). Sensitivity was here defined as the extent to which a species can be altered by a change in temperature. Although the concept is complex[66], part of the species sensitivity can be attributed to the degree of species environmental specialization, which is controlled by the species' genotype[6]. Exposure, which can be approximated using past climatic observations as well as future climatic projections[66], is here defined as the effects of climate change on regional temperatures.

Exposure was the coefficient of variation of annual SSTs calculated for the period 1960–2013 (see Fig. 1d).

Local species extirpation indicates the number of species that is lost locally from a given area. In contrast, local species invasion means the number of species gained.

Quantification of changes in biodiversity. Sensitivity and vulnerability of biodiversity to temperature (annual SST) were assessed by calculating different indices: index of quantitative changes; species turnover; and net qualitative biodiversity changes.

The index of quantitative change was the sum of the differences between theoretical abundance at two time periods weighted by species richness common for the two time periods. This index was calculated for pseudo-species having an abundance higher than 0.1 (a threshold below which the species was considered to be absent) for both periods. For a given geographical cell, quantitative index Q was calculated as follows:

$$Q = \frac{1}{s} \sum_{i=1}^{s} |x_i - y_i|$$

where s is species richness common to the two time periods, x_i is the abundance of species i at the second time period, and y_i is the abundance of species i at the first time period.

In a given geographical cell, species turnover α is the sum of local species invasion G and local species extirpation L, normalized by initial pseudo-species richness R:

$$\alpha = \frac{G + L}{R}$$

Local species invasion is the number of new species found between two time periods, weighted by initial pseudo-species richness (G/R), and local species extirpation is the number of species that is lost between two time periods (L/R), weighted by initial pseudo-species richness. A species is considered to occur in a geographical cell when its abundance is higher than 0.1.

For a given geographical cell, net qualitative biodiversity change β is calculated as the difference between local species invasion G and extirpation L, normalized by initial pseudo-species richness R:

$$\beta = \frac{G - L}{R}$$

When net qualitative biodiversity change is negative, local species extirpation dominates and when it is positive local species invasion dominates.

In the text, 'important' means either that both quantitative and qualitative change, as well as species turnover, are above 5%, or that species local extirpation or invasion is above 2.5% (half the global rate). Other thresholds from 1 to 50% were investigated for both quantitative and qualitative changes and a different threshold would not affect spatial patterns in biodiversity changes (Supplementary Fig. 3).

Sensitivity of biodiversity to a 2 °C change in annual SST. We investigated the theoretical sensitivity of biodiversity to temperature without the effect of exposure and with local changes related only to the intrinsic component of local communities. We estimated biodiversity sensitivity to a uniform temperature rise of 2 °C using average annual SST calculated for 1960–2013 (Fig. 2). In this analysis, exposure (that is, the regional effect of climate change on regional temperature) was not considered exclusively to examine the (intrinsic) sensitivity of biodiversity to temperature.

The first index (quantitative) was the average of all the differences calculated between abundance estimated from mean annual SST (1960–2013) + 2 °C and abundance assessed from mean annual SST (Fig. 2a). This index did not consider the effects of biogeographic movements on local biodiversity (that is, local species invasion or extirpation).

The second index (qualitative) of sensitivity was calculated from the difference between the expected local species invasion (Fig. 2c) and extirpation (Fig. 2b) for each given geographical cell when abundances were calculated from mean annual SST (1960–2013) + 2 °C and mean annual SST for each geographical cell (Fig. 2d). This index therefore considers local changes in biodiversity resulting from biogeographic movements. Both local species invasion and extirpation were normalized by initial pseudo-species richness (G/R and L/R, respectively).

Vulnerability of biodiversity to past climate change. Vulnerability was calculated from mean year-to-year exposure based on the average of all absolute differences in annual SST between one year and the previous for the period 1960–2013 (that is, annual SST + half the amplitude of year-to-year variability for 1960–2013 minus annual SST − half the amplitude of year-to-year variability for 1960–2013; thereby a temperature rise), and from the difference in mean annual SST between both decades 2000–2009 and 1960–1969. The first estimation provides an idea on biodiversity vulnerability resulting from natural year-to-year (high-frequency) variability in temperature (for example, North Atlantic Oscillation[67]), and the second estimation gives an idea on the long-term (low-frequency) decadal vulnerability mainly associated with anthropogenic climate change or long-term natural variability (for example, Atlantic Multidecadal Oscillation[68]).

Expected biodiversity changes related to the average year-to-year variability in annual SST were investigated to examine the influence of this source of variability during the period 1960–2013 (see Fig. 3a–d). For each geographical cell, average year-to-year variability in annual SST was calculated between temperature of a given year and the previous one. We then assessed quantitative changes in biodiversity and both species invasion and extirpation normalized by initial pseudo-species richness (G/R and L/R, respectively) between the average gridded annual SST − half the average year-to-year changes in annual SST and the average gridded annual SST + half the average year-to-year changes in annual SST. Net qualitative biodiversity changes calculated from the difference between the expected local invasion (Fig. 3c) and extirpation (Fig. 3b) for each given geographical cell were also investigated (Fig. 3d).

Expected biodiversity changes between 2000–2009 and 1960–1969 were examined to investigate the recent implications of long-term climate change (natural or anthropogenic) on biodiversity vulnerability (see Fig. 3e–h). We calculated quantitative changes in biodiversity and both species invasion and extirpation normalized by initial pseudo-species richness (G/R and L/R, respectively) between the average gridded annual SST of the period 2000–2009 and 1960–1969. Net qualitative biodiversity changes calculated from the difference between expected local invasion (Fig. 3g) and extirpation (Fig. 3f) for each given geographical cell were also studied (Fig. 3h).

Past and future vulnerability of biodiversity. Changes between the LGM and today were investigated by using the reference period 1960–1969 to exclude the warming that took place after the 1960s, which may be mainly attributed to anthropogenic climate change. Future changes were compared with the reference period 2006–2013 because this period enabled us to study the difference between expected biodiversity based on the same AO-GCM and scenarios. This choice prevented any bias in the difference between the two periods related to the use of a different model, data set or scenario. For the mid-Pliocene, we calculated biodiversity changes between the reference period 2006–2013 and the mid-Pliocene to exclude the warming that took place before 2006 and to use the same reference period as the one chosen for investigating the effect of temperature changes on biodiversity at the end of the century. Biodiversity changes were calculated in such a way that they should be interpreted as biodiversity changes that may occur in the case of a warming with thermal conditions corresponding to those that were observed during the mid-Pliocene. Therefore, biodiversity changes corresponded to a global warming and not a global cooling; this is to be expected when biodiversity changes are calculated between the mid-Pliocene and today. Therefore, all biodiversity changes corresponded to a global warming to facilitate comparisons.

Expected biodiversity changes between 2081–2100 and 2006–2013 were examined by calculating both quantitative and qualitative changes between the end of the century and the time period 2006–2013. These calculations were performed for scenarios RCP2.6, RCP4.5, RCP6.0 and RCP8.5 using five AO-GCMs (only 3 were available for RCP6.0). The same analyses were conducted between the LGM (three data sets) and the 1960s and between the reference period 2006–2013 and thermal conditions corresponding to the mid-Pliocene (only one SST data set; Fig. 4). All quantitative and qualitative biodiversity changes were subsequently latitudinally averaged between 60° S and 60° N to examine the implications for biodiversity in greater detail (Fig. 4g,n).

We quantified oceanic area (in km^2 and percentage) where net quantitative biodiversity changes, species turnover, and net qualitative biodiversity changes (including local species invasion and extirpation) were higher than a threshold ranging from 0 to 50% (Supplementary Fig. 3). We chose a threshold of 5% for all numerical calculations of quantitative and qualitative biodiversity changes (Supplementary Table 1) but changes from 0 to 50% can also be estimated from the examination of Supplementary Fig. 3; for local species invasion and extirpation the threshold was fixed to 2.5% (−2.5% for extirpation and 2.5% for invasion, corresponding to the threshold of 5% for species turnover). Those calculations were performed for changes in biodiversity related to year-to-year variability (1960–2013; Fig. 3a–d), changes in annual SST between 2000–2009 and 1960–1969 (Fig. 3e–h), and changes in biodiversity between 2081–2100 and 1960–1969 (Fig. 4). For future climate scenarios, results are the average of the five AO-GCMs for scenarios RCP2.6, 4.5 and 8.5 and three AO-GCMs for scenario RCP6.0. Biodiversity changes between the LGM and the 1960s were the result of the average of three data sets. Biodiversity changes between the reference period 2006–2013 and thermal conditions corresponding to the mid-Pliocene were based on only one data set. When possible, we assessed the standard deviation of all estimations to provide an assessment of the variation among AO-GCMs or data sets (Supplementary Table 1).

Geographical distances were calculated as follows[69]:

$$d(i,j) = 6{,}377.221 \times h_{i,j}$$

where $d_{i,j}$ is the geographical distance between point i and j, the constant is Earth's radius and $h_{i,j}$ is computed as follows[69]:

$$h_{i,j} = ar\cos(\sin\varphi_i \sin\varphi_j + \cos\varphi_i \cos\varphi_j \cos g)$$

where φ_i is the latitude (in radians) at point i, φ_j is the latitude (in radians) at point j, and g is the difference in longitude between i and j.

Areas where observed (1960–2013; mean year-to-year changes and changes between the 2000s and the 1960s) or projected (2081–2100–2006–2013) biodiversity changes (quantitative changes and species turnover) were higher than those that happened between the LGM and the 1960s and between the reference period 2006–2013 and thermal conditions observed during the mid-Pliocene were quantified (as km^2 and percentage) to provide a better idea on the extent and magnitude of biodiversity changes expected for the end of this century (Table 1).

Correlation analyses. To test whether theoretical patterns were close to observed patterns of biodiversity (crustacean, fish and cetacean), we calculated the coefficient of linear correlation (see Fig. 1a versus Supplementary Fig. 1). As our goal was to model the geographical pattern in biodiversity rather than the exact number of species inside a taxonomic group, we could not compare the number of species expected by the model to the number of species within a taxonomic group. Therefore, we did not use tests commonly applied to examine both the similarity between observed and modelled species richness (for example, the Kolmogorov–Smirnov test or the examination of the regression coefficient from ordinary least-squares regression)[70]. Instead, we used the Pearson coefficient of correlation. To account for spatial autocorrelation in the geographical pattern of species richness (two dimensions), the degrees of freedom were recalculated to indicate the minimum number of samples (n^*) needed to maintain a significant relationship at $p = 0.05$ (refs 20,60,71). The smaller n^*, the less likely is the effect of spatial autocorrelation on the probability of significance[7]. We preferred this technique to others (for example, a technique based on the calculation of the Moran's index or classical semi-variograms) that are based on the assumption of isotropy, which is often violated, as shown on the diversity of North Atlantic calanoid copepods calculated by using (local) point cumulative semi-variograms[69].

When correlation was calculated on time series, the autocorrelation function (ACF) was calculated to allow an adjustment of the actual degree of freedom to more correctly assess the probability of significance of correlations[72]; we labelled this probability p_{ACF} (Supplementary Fig. 2).

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