

# Global change drives modern plankton communities away from the pre-industrial state

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**The ocean—the Earth’s largest ecosystem—is increasingly affected by anthropogenic climate change<sup>1,2</sup>. Large and globally consistent shifts have been detected in species phenology, range extension and community composition in marine ecosystems<sup>3–5</sup>. However, despite evidence for ongoing change, it remains unknown whether marine ecosystems have entered an Anthropocene<sup>6</sup> state beyond the natural decadal to centennial variability. This is because most observational time series lack a long-term baseline, and the few time series that extend back into the pre-industrial era have limited spatial coverage<sup>7,8</sup>. Here we use the unique potential of the sedimentary record of planktonic foraminifera—ubiquitous marine zooplankton—to provide a global pre-industrial baseline for the composition of modern species communities. We use a global compilation of 3,774 seafloor-derived planktonic foraminifera communities of pre-industrial age<sup>9</sup> and compare these with communities from sediment-trap time series that have sampled plankton flux since AD 1978 (33 sites, 87 observation years). We find that the Anthropocene assemblages differ from their pre-industrial counterparts in proportion to the historical change in temperature. We observe community changes towards warmer or cooler compositions that are consistent with historical changes in temperature in 85% of the cases. These observations not only confirm the existing evidence for changes in marine zooplankton communities in historical times, but also demonstrate that Anthropocene communities of a globally distributed zooplankton group systematically differ from their unperturbed pre-industrial state.**

To determine whether anthropogenic climate change has affected the marine environment beyond its natural state, it is essential to compare modern observations to a pre-industrial baseline. Because such a baseline is available for the physical state of the ocean, it has been established that, in response to global warming, the sea-surface temperature field has changed significantly since the onset of industrialization approximately 170 years ago<sup>1,2</sup> (Fig. 1). Marine ecosystem research, on the other hand, is almost exclusively based on observations since the mid-twentieth century and the pre-industrial baseline is therefore mostly unknown. Although existing observations provide strong evidence for changes in marine ecosystems in a direction that is consistent with late-twentieth century climate change<sup>3,4,10,11</sup>, this lack of a pre-industrial reference prevents assessing the degree to which Anthropocene marine ecosystems differ from their natural, pre-industrial state<sup>12</sup>. This affects our ability to predict the effects of global change on marine ecosystem functioning and the resulting impacts on the resources that they provide to society.

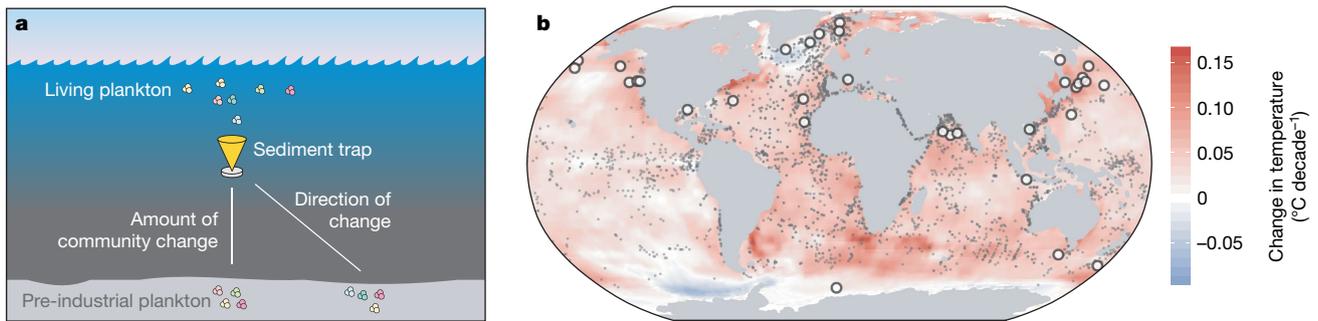
Planktonic foraminifera are a globally ubiquitous group of marine zooplankton. Their distribution is primarily controlled by temperature<sup>13,14</sup>. About 40 morphospecies are known<sup>15</sup>; they occur most abundantly in the surface mixed layer, but some species can be found alive down to several hundreds of metres<sup>16</sup>. They are unique among marine zooplankton because their calcite shells are well-preserved in marine sediments. This renders them an ideal model system to investigate the

influence of global change on marine zooplankton, because seafloor sediments offer the chance to obtain an accurate picture of the composition of planktonic foraminifera communities in the past. Indeed, their skeletal remains have extensively been used to elucidate past climate and ecological changes<sup>17,18</sup>. However, the influence of anthropogenic climate change on planktonic foraminifera communities has only been investigated in very few studies with a regional focus<sup>7,19</sup> and an assessment on a global scale is lacking.

Here we use a quality-controlled compilation of planktonic foraminifera species assemblages of pre-industrial age from seafloor sediments (see Methods) and compare these to modern (1978–2013) assemblages based on observations from moored sediment-trap time series (see Methods). The sediment samples ( $n = 3,754$ ) cover all major ecological provinces, and almost the entire global temperature gradient, at high resolution (Fig. 1). By virtue of the sedimentation process and sediment mixing by deep-sea organisms, foraminiferal shells that are extracted from the uppermost sediment layer represent a centennially to millennially integrated assemblage before marked human influences (see Methods). The modern assemblages are based on the integration of shell flux of planktonic foraminifera over at least one year and are thus not affected by ontogeny and/or seasonality. Most of the sediment-trap sites are from the Northern Hemisphere; however, they cover the global thermal gradient and include time series spanning up to 12 years. We compare these Anthropocene assemblages with those in the sediment using a square-chord distance metric on species relative abundances (see Methods). We find that all Anthropocene communities differ from those in the nearest sediment sample and that the degree of dissimilarity scales with the temperature change since AD 1870 at each site ( $r = 0.53$ ,  $P = 0.001$ ,  $n = 33$ ; Fig. 2a). This suggests that planktonic foraminifera communities have changed considerably since the pre-industrial period, and that they have done so in proportion to the magnitude of local temperature change. When comparing the modern species composition with the sediment samples, we find that for each modern assemblage the most similar sedimentary analogue is not the assemblage from the nearest core top, but an assemblage from a core top located elsewhere (Fig. 2b). Thus, the changes in community composition and presence of close analogues elsewhere indicate a directional shift at the community level, rather than a random reshuffling of the species forming previously unseen communities. On the basis of the difference between the modern and pre-industrial communities, we estimate that this shift equates to a median latitudinal displacement of 602 km (range, 45–2,557 km) since pre-industrial times (Fig. 2c).

To evaluate the direction of change in community composition, we consider the location of sedimentary assemblages with species compositions that are most similar to the Anthropocene assemblages from the sediment traps. We observe that these sediment assemblages are in most cases from warmer areas, thus confirming that the twentieth-century community composition shows an imprint of global warming (Fig. 3). Warming signatures are found across the globe and in a range

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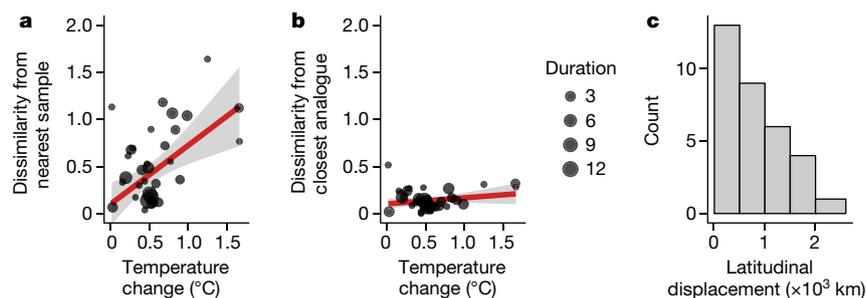
**Fig. 1 | Concept of the comparison between Anthropocene and pre-industrial communities.** **a**, The integrated living planktonic foraminifera flux from sediment-trap time series is compared to the sedimentary community closest to the trap to quantify community change. The position of the most-similar sedimentary assemblage reveals the direction

of the change. **b**, Grey and white dots indicate the position of the sediment samples and sediment traps, respectively. Background shows the linear sea-surface temperature trend between 1870 and 2015 based on the Hadley Centre Sea Ice and Sea Surface Temperature dataset (HadISST)<sup>26</sup>.

of environments (open ocean, coastal regions, upwelling regions, and at low and high latitudes), which indicates that species compositions have shifted worldwide. Some parts of the ocean are known to have been cooling during the Anthropocene (Fig. 1). This historical cooling has also affected the composition of Anthropocene assemblages, such that the direction of change inferred from the change in the planktonic foraminifera community is—in the large majority of cases (85%)—consistent with the observed temperature change, irrespective of whether the observed historical trend has been warming or cooling (Fig. 3). The single case in which the species composition indicates warming in a cooling area is in the North Pacific gyre, where the amount of temperature change has been negligible. Thus, we conclude that the chance of finding false warming signatures is low and that the observed pattern in community change is robust, indicating that the communities have responded to the dynamic pattern of changes in sea-surface temperatures induced by global warming. We also observe that time series that show a change in the species community that is inconsistent with historical changes in temperature, are randomly distributed throughout the observational period. Therefore, there is no trend in the degree of consistency, which suggests not only that the faunal composition departed from the pre-industrial baseline but also that it started to do so before the beginning of the sediment-trap observations in AD 1978. If we assume that the inferred community change occurred predominantly after the mid-nineteenth century onset of industrial-era warming, the observed median displacement of approximately 600 km translates into a displacement rate of around 40 km per decade. This is a conservative estimate, because it is likely that the rate of community change accelerated during the twentieth

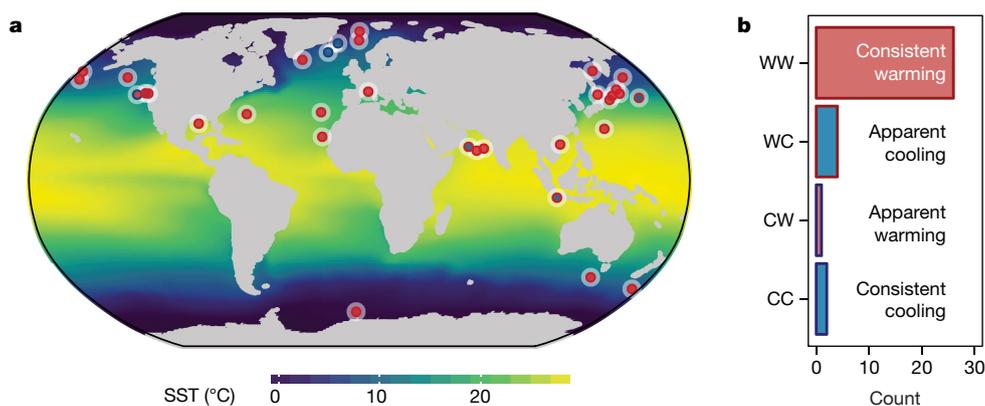
century and—although there are no comparable data on the rate of community displacement—our estimate is comparable to displacement rates of individual zooplankton species (around 100 km per decade)<sup>3</sup>.

Even though the pattern of community change in the planktonic foraminifera shows a clear fingerprint of global warming, comparisons between assemblages from the plankton and from the sediment are not straightforward. By using direct observations of integrated annual flux from sediment traps, we obtained a more realistic approximation of sedimentary assemblages than indirect estimates from repeated plankton tows because the effects of ontogeny and seasonal abundance variability can be ruled out. Nevertheless, we also evaluate the effect of other potential biases on our observations, in part because some of the variance in the assemblage change remains unexplained (Fig. 2a). We rule out a temporal sampling bias due to interannual variability as, firstly, the sign of change in individual years is consistent with the long-term signal in 81–92% of the multiyear time series (Fig. 4a) and, secondly, the signal is consistent in 87% of the one-year time series, which should otherwise mostly be affected by noise imposed by interannual variability. The comparisons between modern and pre-industrial assemblages could furthermore be complicated by differential preservation in the sediment<sup>20,21</sup> and the non-uniform spatial distribution of the sediment samples. We therefore perform sensitivity tests using subsets of the data. We use depth as an indicator of potential preservation bias, as calcite dissolution increases with water depth, and choose 2,000 m as a level below which the assemblages could be affected by dissolution. This is a conservative separation even for the Pacific Ocean, where the lysocline is shallower than in the Atlantic Ocean<sup>22</sup>. As foraminifera can



**Fig. 2 | Changes in planktonic foraminifera communities in response to Anthropocene sea-surface temperature change.** **a**, Dissimilarity to the nearest sediment sample, indicative of the compositional difference between modern and pre-industrial communities, scales with the absolute historical change in temperature at the site of each trap ( $n = 33$ ;  $r = 0.53$ , weighted by time-series duration,  $P = 0.001$ ; unweighted  $r = 0.48$ ,  $P = 0.005$ ), which suggests that species composition has changed proportionally to temperature change since pre-industrial times. **b**, Dissimilarity between modern and most-similar

pre-industrial species communities, showing that all Anthropocene species communities have more similar analogues elsewhere (difference between **a** and **b**), consistent with a shift of the species composition in the same direction as the temperature change. **a**, **b**, Dots are scaled to the duration of the sediment-trap time series; error envelopes show 95% confidence intervals. **c**, Histogram of latitudinal displacement of planktonic foraminifera communities in kilometres since pre-industrial times (see Methods).



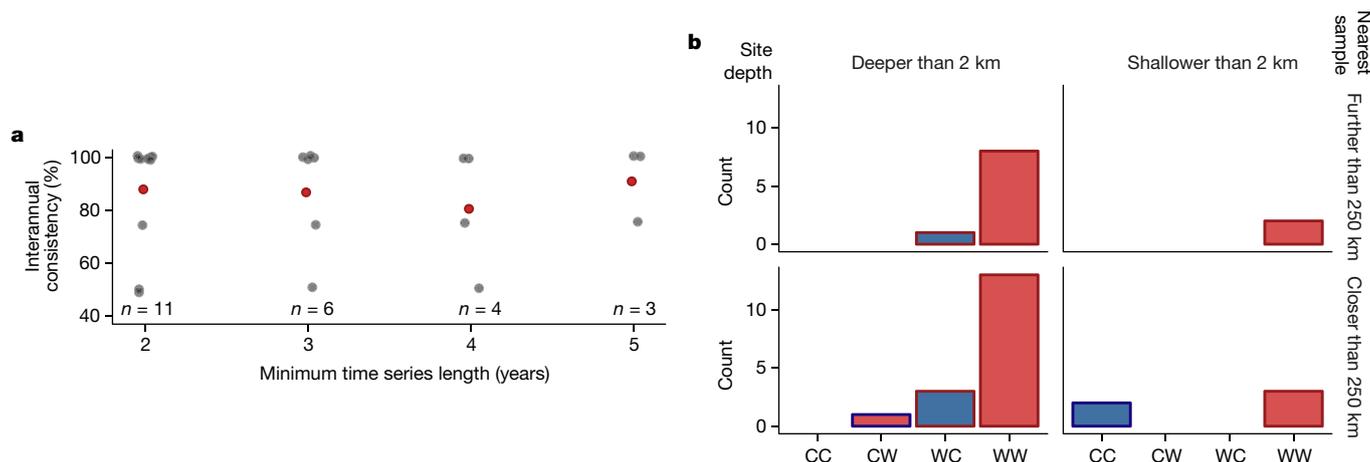
**Fig. 3 | Global planktonic foraminifera communities change consistently with historical temperature trends.** Planktonic foraminifera community change shows a clear predominance of warming signatures across the oceans, consistent with the known pattern of Anthropocene sea-surface temperature change. **a**, Spatial pattern of the direction of community change (colour fill) and the direction of the historical change in temperature (border colour); both agree in 85% of the observations

( $P < 0.001$ , two-sided binomial test,  $n = 33$ ). Background colour shading shows mean sea-surface temperature (SST)<sup>26</sup> over the observation period (1978–2013). **b**, Histogram of the consistency of Anthropocene community change in response to temperature change. W and C indicate warming and cooling, respectively. The first letter indicates the historical change, and the second indicates change in the species composition.

be transported by ocean currents over hundreds of kilometres during their life cycle and while sinking to the seafloor<sup>23,24</sup>, we use a 250-km threshold to separate modern samples with a far and nearby pre-industrial counterpart. All four subsets show that in the majority of the cases the direction of change in species communities is consistent with historical temperature change (Fig. 4b). Finally, we also evaluated the sensitivity of our results to the effect of differences in size fractions used to determine the community composition and to the uncertainty in the observational temperature data (see Methods). These tests also confirm that the observed pattern in global planktonic foraminifera community change is robust.

We thus show that there is a globally expressed difference between pre-industrial and Anthropocene marine planktonic foraminifera communities that indicates community turnover, which is in sign and magnitude consistent with global temperature change. As such, we provide evidence in support of observations from shorter time series that lacked a characterization of community state before human influence<sup>3–5</sup>. The community change in planktonic foraminifera unambiguously shows

that human influence has considerably altered their species communities across the globe. This has important implications for the calibration of palaeoclimate proxies based on planktonic foraminifera, because foraminifera that are preserved in the sediment no longer reflect oceanographic conditions above the site of deposition. We also suggest that the described shifts in planktonic foraminifera are indicative of a more-general phenomenon across marine ecosystems, in which present-day assemblages differ from historical ones in a way that reflects the change in environmental conditions since the onset of the Anthropocene. These findings place emphasis on the recent discussion on how well communities are adapted to rapid environmental change: if the potential for spatial displacement and adaptation lags behind the rate of change in the environment, modern-day assemblages may always show a trait distribution with suboptimal fitness<sup>25</sup>. Beyond single species, this lag may be especially explicit at the level of communities given the time needed to establish new interaction networks. This, in turn, has potentially large effects on ecosystem functioning as well as on the services that marine ecosystems deliver to society.



**Fig. 4 | Robustness of the sign of change in planktonic foraminifera community composition.** **a**, Proportion of individual years in multi-year time series that show a community change consistent with the long-term mean (grey dots, jittered for visibility, show individual time series; red dots show the mean). We restricted this analysis to time series with a duration of at least two years and years without gaps longer than three months. On average, 81–92% of the individual years are consistent with the long-term average and this consistency is robust against time-series length and

imputation. This indicates that our observations are not biased by single anomalous years but instead reflect a robust change in global species composition. **b**, Sensitivity tests show that our results are not dependent on differential preservation and non-uniform spatial distribution of the sediment samples, as each subset is dominated by changes in the species community that are consistent in sign with historical changes in temperature. Labels are as in Fig. 3b.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1230-3>.

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**Author contributions** L.J. and M.K. designed research. L.J. compiled and analysed the data. All authors discussed the results and contributed to the writing of the manuscript.

**Competing interests** The authors declare no competing interests.

### Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41586-019-1230-3>.

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## METHODS

**Data.** Quality-controlled and taxonomically harmonized core top assemblage data were obtained from the ForCenS dataset<sup>9</sup>. Samples for which species groups and species forms (for example, differently coiled morphospecies) were not resolved were excluded ( $n = 128$ ) and in cases in which multiple samples were available for the same location ( $n = 303$ ), one was randomly selected. The modern assemblages are derived by integrating shell flux time series from moored sediment traps (Extended Data Table 1). Sediment-trap time series selection criteria followed a previous study<sup>27</sup> with the additional constraint that only time series with full taxonomic resolution (considering the same range of species as in the sediment samples) were included. The taxonomy of the time series was harmonized with that of the core top data following previously published criteria<sup>9</sup>. To eliminate the effect of seasonality in the flux when deriving the flux-weighted assemblages, only time series with a length of at least 345 days were analysed. Gaps in the time series were linearly interpolated or, where possible, filled using a smoothed version (LOESS, span 0.1) of the multiyear median flux pattern. To make full use of the available data and to estimate the influence of interannual flux variability, annual assemblages were calculated for each year for which at least three months of data were available, using the smoothed flux pattern to impute missing values. As is common in palaeo-ecological studies, the dissimilarity between the pre-industrial and modern species assemblages was assessed using square chord distance between species relative abundances because this metric has been shown to be most effective in identifying analogues in microfossil datasets<sup>28</sup>.

Various planktonic foraminifera morphospecies consist of multiple, genetically different, cryptic species<sup>29</sup>. To minimize the effect of differences in the ecology of cryptic species, dissimilarity was determined regionally<sup>18</sup> such that sediment samples with the most-similar assemblages were sought only within the same oceanic basin as the analysed sediment-trap time series.

The latitudinal displacement of the species communities was estimated from the dissimilarity between the modern assemblage and the nearest sediment assemblage. We used linear relationships between dissimilarity and the latitudinal component of distance derived from the sediment data. To account for regional variability in spatial trends in biodiversity, we established these relationships for each sediment trap site, using the latitudinal distance from the nearest sediment sample within a radius of 5,000 km. Regression models were forced through the origin (because at zero distance, the assemblages should be identical) and established for the first 2,500 km latitudinal distance, as this is the distance at which dissimilarity tends to saturate and the distance–dissimilarity relationship changes slope (see example in Extended Data Fig. 2).

Sea-surface temperature data are from the HadISST dataset<sup>26</sup>. We use data from the 1870–1899 period within a 100-km radius around each sampling location to derive an estimate of the mean temperature. The direction of historical change in temperature for each sediment-trap location was derived from the difference between the mean temperature at the time of sediment-trap sample collection and the late-nineteenth-century mean. This temperature change provides an estimate of the temperature change at each site that is indicative of warming or cooling since approximately the beginning of industrial-era warming. However, given the uncertainty in the age of the sedimentary species assemblages, it is only an approximation of the temperature change since the time of deposition of the sediments. We nevertheless consider this adequate for the purpose of our analysis.

All analyses were done in R<sup>30</sup> using packages rioja<sup>31</sup>, reshape2<sup>32</sup>, ggplot2<sup>33</sup>, geosphere<sup>34</sup>, readxl<sup>35</sup>, Hmisc<sup>36</sup>, raster<sup>37</sup>, sp<sup>38,39</sup> and rgdal<sup>40</sup>.

**Pre-industrial age of core tops.** Marine-sediment archives provide a temporally integrated record of species assemblages. The length of this record depends on the sampling resolution, the sediment accumulation rate and the depth of the layer mixed by bioturbation. The mean age of the core top samples can thus be estimated using the depth solution of a previously published study<sup>41</sup> and reasonable approximations of the sediment accumulation rate and bioturbation depth. Using an empirical relationship between water depth and Holocene sediment accumulation rate<sup>42</sup>, we calculate a median sediment accumulation rate of the core top samples of 5.9 (interquartile range, 3.8–6.2) cm per thousand years. For bioturbation depth, we use a global average<sup>43</sup> of  $9.8 \pm 4.5$  cm. These analyses yield estimated mean ages of the core top sediments of centuries to millennia, warranting their use as an integrated pre-industrial baseline of the planktonic foraminifera assemblages (Extended Data Fig. 1). Note that Extended Data Fig. 1 provides the average age of non-normal distribution of the ages of all sedimentary particles (including foraminifera), such that all sediments also contain foraminifera within the age range of the temperature estimates before marked human influences.

**Effect of shell size.** Planktonic foraminifera differ in their mean size among species and species assemblages may therefore vary as a function of the analysed size fraction. Whereas the core top samples are all  $> 150 \mu\text{m}$ , our shell flux time series compilation also includes data for sizes  $> 125 \mu\text{m}$ . Even though cold-water species are more abundant in smaller size fractions<sup>44</sup> and inclusion of data for sizes of

$< 150 \mu\text{m}$  would thus bias our results towards cooling rather than warming we nevertheless assessed the influence of size fraction in two ways.

First, we included an additional sensitivity test for the consistency of community change (analogous to Fig. 4) separating the time series by size fraction (Extended Data Fig. 3). Both groups show a change in the community composition consistent with temperature change in the large majority of the cases, which indicates that our results are insensitive to the size fraction of the foraminifera in the sediment-trap time series.

Second, we carried out separate analyses of the coarse- and fine-fraction data from the seven time series for which size-fractionated data are available (CAS, CCG, CCM, CCN, EAS, MBL and WAS; see Extended Data Table 1 for details). In 6 out of these 7 cases, the direction of community change indicated by the assemblages  $> 125 \mu\text{m}$  is identical to the change estimate from the assemblages  $> 150 \mu\text{m}$ , or indicative of cooling. This means that inclusion of data from time series with the small-size fraction data are much more likely to suggest cooling than warming.

Importantly, the two cases of a consistent shift towards cooler assemblages both pertain to data from the  $> 150\text{-}\mu\text{m}$  fraction (Extended Data Table 1) and hence do not reflect size-related biases. The pattern of assemblage change is therefore a robust, if conservative, estimate of the change in planktonic foraminifera community change.

**Effect of choice of temperature dataset.** Historical sea-surface temperature data that predate the onset of large-scale shipboard measurements and satellite observations are associated with uncertainty, which is reflected in the differences between different data products. To evaluate the effect of the choice of temperature data product, we also conducted our analysis using ERSST version 5 data<sup>45</sup>. Compared to the HadISST data, ERSST data have a coarse resolution ( $2^\circ \times 2^\circ$  compared to  $1 \times 1^\circ$ ), but the data extend back to AD 1854, offering the possibility to obtain a better estimate of industrial-era warming. The ERSST v.5 data (also integrated over 30 years, but shifted backwards to AD 1854 to make full use of the longer temporal extent of the ERSST data) show generally less temperature change compared to HadISST<sup>46</sup>. However, our results are largely insensitive to the data product used and the two sea-surface temperature products reveal the same patterns. The scaling between dissimilarity and temperature change is similar, albeit with a larger uncertainty for ERSST (Extended Data Fig. 4a), and the changes in species community are also largely consistent with the temperature change estimated from the ERSST data (Extended Data Fig. 4b). This makes us confident that the observed patterns in the change in species communities are robust.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

## Data availability

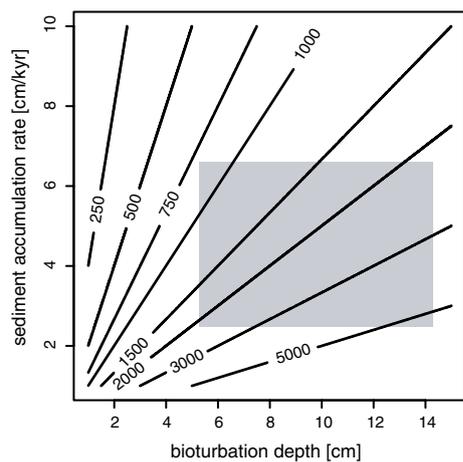
The ForCenS core top planktonic foraminifera dataset is available at Pangaea (<https://doi.org/10.1594/PANGAEA.873570>) and the HadISST data are available from the UK Met Office (<https://www.metoffice.gov.uk/hadobs/hadisst/>). NOAA ERSST v.5 data were provided by the NOAA/OAR/ESRL PSD (<https://www.esrl.noaa.gov/psd/>). Taxonomically harmonized shell flux data are available at <https://doi.org/10.5281/zenodo.2638013>.

## Code availability

Code is available at <https://doi.org/10.5281/zenodo.2638013>.

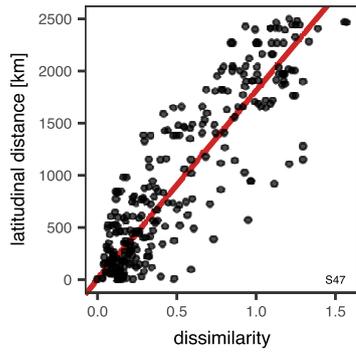
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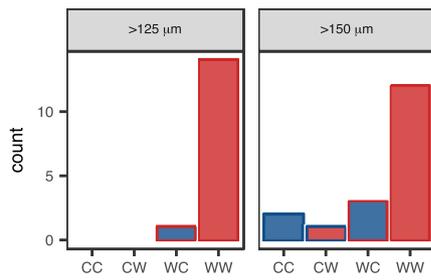


**Extended Data Fig. 1 | Pre-industrial age of the sedimentary samples.**

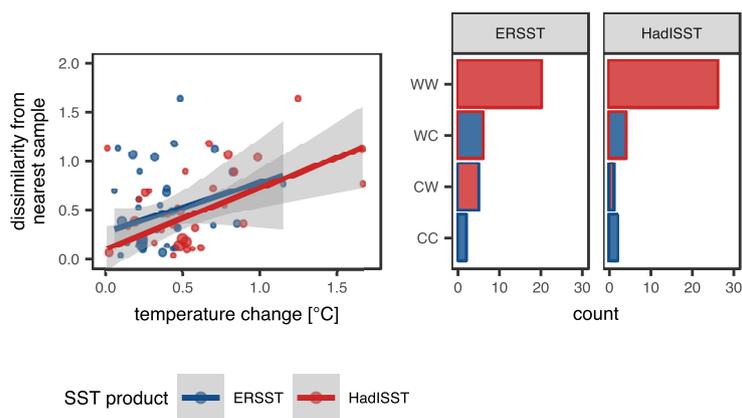
Mean age in years of core top sediment estimate using the depth solution of a previous study<sup>41</sup> (contours). The grey box denotes the likely average ages of the core top sediments based on our best estimate of sediment accumulation rate (in cm per 1,000 years (kyr)) and bioturbation depth. Irrespective of the sampling date (mostly pre-1980), the average sedimentary species composition predates the Anthropocene.



**Extended Data Fig. 2 | Linear regression between dissimilarity and latitudinal distance in the sedimentary species assemblages.** The relationship (shown in red) is used to estimate the latitudinal displacement based on the dissimilarity between the modern and pre-industrial species composition. Example for time series S47 from the south of New Zealand (Extended Data Table 1).



**Extended Data Fig. 3 | Insensitivity of planktonic foraminifera assemblage change to size fraction.** The direction of change for planktonic foraminifera species communities (warming or cooling) was inferred from sediment-trap time series for which the samples were larger than 125  $\mu\text{m}$  and larger than 150  $\mu\text{m}$ . Colours and symbols are as in Fig. 3b. W and C indicate warming and cooling, respectively, with the first letter indicating the historical change and the second the change as indicated by the species composition. Both small and large shell sizes are dominated by a change in the species community that is consistent with the direction of historical change in temperatures. The observed pattern is thus insensitive to the inclusion of sediment-trap time series that used a slightly smaller size fraction than the sediment samples.



**Extended Data Fig. 4 | Assessing uncertainty in the historical change in temperatures by comparing the HadISST and ERSST temperature products.** **a**, Comparison of the relationships between the historical change in temperature and the difference between the modern and sedimentary species composition (based on linear regression weighted to the duration of the time series; see also Fig. 2a). The relationship has a similar slope for both sea-surface temperature products, even though the

relationship based on ERSST data has a larger uncertainty. Shaded error envelopes show 95% confidence intervals of the regression. **b**, Histograms of consistency and direction of changes in the species communities (Fig. 3a). The pattern of change is broadly similar for both products, which indicates that although the observations are to some degree sensitive to the uncertainty in the historical change in temperatures, they are largely consistent between the two datasets.

Extended Data Table 1 | Sediment-trap time series used to determine modern species compositions

Name	Longitude [east]	Latitude [north]	Water depth [m]	Duration [days]	Minimum size [ $\mu\text{m}$ ]	Reference	Change*
ABP	-177.00	53.05	3788	3265	125	47	WW
BAT	-64.25	32.08	4200	2233	125	48, 49	WW
CAP	174.15	-52.62	2580	426	150	50	WW
CAS	64.75	14.47	3900	503	150	51	WW
CBL	-20.69	21.15	4150	389	150	52, 53	WW
CCG	-132.02	41.54	3664	364	150	54	CW
CCM	-127.58	42.19	2830	352	150	54	WC
CCN	-125.77	42.09	2829	360	150	54	WW
EAS	68.75	15.47	3770	528	150	51	WW
GLS	0.00	75.00	3720	346	125	55	WW
GOM	-90.30	27.50	1300	431	150	56-58	WW
ILP	-16.00	68.00	1231	352	150	59	CC
IRM	-38.5	59.00	3000	380	150	60-62	WW
JAM	108.00	-8.25	3060	984	150	63	WC
LPL	5.18	43.02	1000	4459	150	64	WW
MAU	-2.50	-64.90	5023	1133	125	65	WW
MBL	-22.00	33.00	5500	762	150	66	WW
MRI	-22.00	63.00	833	352	150	59	CC
NBA	-0.47	69.69	3270	444	125	55	WW
NP4	165.00	40.00	5483	953	125	67	WC
NP5	165.00	50.00	5570	1288	125	67	WW
NPK	155.00	44.00	5370	894	125	67	WW
NWP	141.87	41.56	970	361	125	68	WW
OKH	149.85	53.32	1166	365	150	69	WW
PAP	-145.00	50.00	4256	1438	125	70	WW
S47	142.00	-46.80	4571	494	150	71	WW
SAP	-174.00	49.00	5406	3268	125	47	WW
WAS	60.47	16.32	4015	529	150	72	WC
WC1	137.00	25.00	5100	613	125	73	WW
WC2	147.00	39.00	5335	629	125	73	WW
WC5	150.00	40.97	5615	358	125	74	WW
WC6	155.24	42.01	5578	382	125	74	WW
XTS	110.87	17.43	1694	790	154	75	WW

Data were obtained from previous studies<sup>47-75</sup>.

\*The first letter refers to the historical temperature change, and the second letter refers to the change indicated by the change in the species composition. W and C indicate warming and cooling, respectively.

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The ForCens core top planktonic foraminifera data set is available at Pangaea (<https://doi.pangaea.de/10.1594/PANGAEA.873570>) and the HadISST data are available from the UK Met Office (<https://www.metoffice.gov.uk/hadobs/hadisst/>). NOAA ERSST V5 data were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at <https://www.esrl.noaa.gov/psd/>. Code and taxonomically harmonised shell flux data will be made available on github/zenodo.

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Study description	We compare species communities (relative abundances) of fossil and modern marine microplankton (planktonic foraminifera) using commonly used dissimilarity metrics. Data on the modern species communities is derived from sediment traps and fluxes have been integrated to allow comparison with the fossil data. The approach is described in the method section.
Research sample	We used published data only; fossil species community data from Siccha, M., and Kucera, M.: ForCenS, a curated database of planktonic foraminifera census counts in marine surface sediment samples, Scientific Data, 4, 170109, 10.1038/sdata.2017.109, 2017. We chose this dataset as it is the most extensive and most recent compilation to date. Sediment trap data were compiled from literature (see Jonkers, L., and Kučera, M.: Global analysis of seasonality in the shell flux of extant planktonic Foraminifera, Biogeosciences, 12, 2207-2226, 10.5194/bg-12-2207-2015, 2015.). We have updated this compilation in order to include all (to the best of our knowledge, see also reviews) sediment trap time series. A full list is provided in the method section of the manuscript
Sampling strategy	We used compiled literature data
Data collection	We used previously compiled and published data, collection methods are described in the relevant publications listed in the method section
Timing and spatial scale	We used previously published data. The fossil data are from surface deep sea sediments sampled over the past decades (age assessed in manuscript) and the modern data from moored sediment traps are from over 30 different studies since 1978. Both data sets are global in their extent
Data exclusions	Criteria for inclusion in our shell flux compilation were predetermined and 1) a minimum time series length of 345 days in order to reduce the effect of seasonality; 2) complete taxonomic resolution in order to sensibly compare plankton and sediment species assemblages and 3) no indication of resuspension (i.e. the presence of benthic foraminifera) to make sure that we are looking at a primary signal.
Reproducibility	no experiments conducted
Randomization	no experiments conducted; not applicable to observational time series from sediment traps used here
Blinding	no experiments conducted; not applicable to observational time series from sediment traps used here
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