Cyclic evolution of phytoplankton forced by changes in tropical seasonality

Luc Beaufort[1]*, Clara T. Bolton[1]*, Anta-Clarisse Sarr[1], Baptiste Suchéras-Marx[1], Yair Rosenthal[2], Yannick Donnadieu[1], Nicolas Barbarin[1§], Samantha Bova[3], Pauline Cornuault[1#], Yves Gally[1], Emmeline Gray[1&], Jean-Charles Mazur[1], Martin Tetard[1]

[1]Aix Marseille Univ, CNRS, IRD, INRAE, Coll France, CEREGE, Aix-en-Provence, France
[2]Rutgers University, Piscataway, USA
[3]Department of Geological Sciences, San Diego State University, San Diego, California, USA
[§]Present address: TOTAL S.A., Pau, France
[#]Present address: Universität Bremen, MARUM, Bremen, Germany
[&]Present address: The Open University, Milton Keynes, UK
* To whom correspondence should be addressed: beaufort@cerege.fr or bolton@cerege.fr

Although the role of Earth's orbital variations in driving global climate cycles has long been recognised, their effect on evolution is hitherto unknown. Because of their abundance in marine sediments and preservation of their morphological adaptation to the changing environment[1], the fossil remains of coccolithophores, a key calcifying phytoplankton group, enable an exceptional assessment of the impact of cyclic orbital-scale climate changes on evolution[2]. Recently, evolutionary genetic analyses linked broad changes in Pleistocene fossil coccolith morphology to species radiation events[3]. Using high-resolution coccolith data, we show that during the last 2.8 million years the morphological evolution of coccolithophores was forced by Earth's orbital eccentricity with rhythms of ~100,000 years and 405,000 years - a distinct spectral signature to that

of coeval global climate cycles[4]. Simulations with an Earth System Model[5] coupled with an ocean biogeochemical model[6] demonstrate strong eccentricity modulation of the seasonal cycle, which we suggest directly impacts the diversity of ecological niches occurring over the annual cycle in the tropical ocean. Reduced (enhanced) seasonality favours species with mid-size (large and small) coccoliths, increasing (decreasing) coccolith carbonate export and burial. We posit that eccentricity pacing of phytoplankton evolution contributed to the strong 405-kyr cyclicity seen in global carbon cycle records.

Coccolithophores produce half of the biogenic $CaCO_3$ in the open ocean[7] and their fossil platelets (called coccoliths) first appeared in sediments during the Upper Triassic, ~215 million years ago (Ma). Thereafter, coccolithophores rose to dominance[8] and became a key biological modulator of the global carbon cycle via photosynthesis and calcification[9]. In the dominant Cenozoic Noelaerhabdaceae family (including *Emiliania huxleyi* and *Gephyrocapsa*), species are defined by the morphological characteristics of their coccoliths, with size being a key criterion[10] that is related to cell size[11]. For *Gephyrocapsa* and *Emiliania*, phylogenies reconstructed from gene sequences indicate that morphology-based definitions correspond to biological species[3,12]. Within a given Noelaerhabdaceae population, typically dominated by one but including several species, interspecific and intraspecific changes in coccolith length and mass occur in response to environmental parameters such as carbonate chemistry[1] and temperature[2]. Studies of coccolithophore evolution have focused on geological-timescale changes in species richness and turnover[13], coccolith carbonate accumulation[8,14], or calcification potentially driven by carbon cycle changes[15]. In addition, climate changes induced by orbital cycles (on timescales of tens to hundreds of thousands of years) strongly influence nannofossil assemblage composition (e.g. references 16-18).

However, to date the impact of orbital cycles on coccolithophore evolution, coccolith morphology, and carbonate production have not been explored simultaneously.

Here, we quantify the Pleistocene history of tropical Noelaerhabdaceae evolution at high resolution (~2 thousand years, kyr), using coccoliths preserved in nine well-dated sedimentary sections from the Indian and Pacific Oceans cored during International Ocean Discovery Program (IODP) and International Marine Past Global Changes Study (IMAGES) expeditions (Extended Data Table 1). We use artificial intelligence microscopy to create an unprecedented biometric database of over 7 million coccoliths from >8000 samples (see Methods). The strong similarity of morphometric patterns observed at each site (Extended Data Fig. 1) has led us to build composite frequency contour plots of coccolith size and mass, representing larger-scale evolutionary change (Fig. 1a, Methods). Patches denoting high frequency of a particular size correspond in many cases to described acmes of Noelaerhabdaceae species[19-21] or proposed evolutionary events[3] (Fig. 1). The most recent evolutive phase starting ~550 thousand years ago (ka) is attributed to a radiation event and the emergence of new *Gephyrocapsa* species, based on a genetic study of extant taxa and its temporal correlation to low-resolution coccolith morphometric data[3]. Over the Pleistocene, average coccolith size shows an increasing trend that corresponds to a gradual shift in dominance from smaller to larger coccoliths (Fig. 1b). On orbital time scales, global ice volume and deep-sea temperature as represented by benthic foraminiferal $\delta^{18}O$[22] show a dominance of 41-kyr and later ~100-kyr glacial-interglacial cycles (Fig. 1c)[22]. In contrast, average coccolith length follows a regular cycle that is highly coherent (>99.9%) with the orbital eccentricity periods of 405 kyr (e405) and of 124 and 95 (e100) [23] (Extended Data Figure 2a), with larger average size occurring at high eccentricity with a slight time lag (Fig.

1b).

Average size or mass of coccoliths in a Noelaerhabdaceae population may vary because of macro- and/or micro-evolution, or because ecological changes modulate the relative abundances of species in different size ranges. To build a metric that describes only species evolution, we remove the effect of relative abundance changes related to ecology[24] by formulating a Morphological Divergence Index, MDI, calculated as the difference in average coccolith mass between two size classes, larger and smaller than 3 μm (Methods). Thus, MDI quantifies morphological divergences of species over time through evolution, and could be driven by changes in size or degree of calcification (see Fig. 2 for a conceptual explanation). Noelaerhabdaceae coccolithophores spread rapidly throughout the oceans and are often cosmopolitan, resulting in the same species being present in many regions, but with different relative abundances[12,19]. MDI varies independently of regional ecological specificities, and MDI records from sites in distinct oceanographic biomes[25] and climatic regimes (e.g., warm pool, monsoon-dominated; Extended Data Table 1) are highly intercorrelated, all showing significant e405 and e100 periods (Extended Data Figures 1, 2). Therefore, we produce a composite MDI stack, preserving the high resolution of each dataset (Fig. 1e, Methods). The MDI stack, interpreted as reflecting evolutionary changes in morphological diversity, shows strong 405-kyr pacing throughout the Pleistocene irrespective of glacial-interglacial background state. Cross-spectral analysis indicates significant (>90%) coherency between the stack and Earth's eccentricity periods since 2.8 Ma (Fig. 1d, d'). This pattern cannot be the result of differential dissolution on coccolith morphology (see Methods) since in contrast to MDI, Pleistocene deep-sea $CaCO_3$ dissolution generally follows a glacial-interglacial cycles[26]. Similarly, coccolith morphological evolution appears not to be not responding directly to physical parameters covarying with global ice volume, such as sea level or ocean temperature. While eccentricity forcing on coccolithophore productivity has previously been suggested[27,28], our new dataset reveals that eccentricity cycles instead forced the evolution of the Noelaerhabdaceae.

Cyclic coccolithophore evolution may have impacted the ocean carbon cycle via coccolith carbonate production and burial in sediments [14,29]. Coccolithophores produce large amounts of calcite during blooms [27,30], and sediments are often dominated by few opportunistic species, for example *Emiliania huxleyi* (0-90 ka)[19] and *Gephyrocapsa caribbeanica* (280-570 ka)[20] in the late Pleistocene. We estimate the mass accumulation rate of Noelaerhabdaceae coccoliths (NoMAR) in our cores and produce a stacked record (Fig. 1g, Methods). Noelaerhabdaceae coccoliths represent on average half of the total calcareous nannoplankton mass in our studied cores (Extended Data Table 2). The two components of NoMAR, coccolith flux and average mass, are separated in Extended Data Figure 3. This reveals that NoMAR is primarily driven by changes in coccolith flux, and that flux and mass often have opposing effects on NoMAR since medium-sized, lighter species (e.g., *E. huxleyi*, *G. caribbeanica*) contribute the most to coccolith carbonate export. Thus, higher NoMARs when mid-size opportunistic species dominate often correspond to lower MDI values (Fig. 1e, g). The dominance of these opportunistic species coupled with high coccolithophore accumulation in sediments during eccentricity minima is also recorded in the extra-tropics[27]. In contrast to MDI, local ecological conditions affecting productivity and export, and possibly water depth affecting coccolith accumulation, also influence NoMAR, thus a linear relationship between the two is not expected. Though it is impossible to quantify the relative effects of these factors, common trends between sites emerge despite different absolute values, and these trends are reflected in the NoMAR stack. Thus, NoMAR combines global evolutionary and local ecological drivers of calcite production, while MDI should exclusively record evolution. Nevertheless, the NoMAR composite record shows strong eccentricity periodicities that are significantly coherent with MDI throughout the Pleistocene (Fig. 1f, f'), demonstrating a strong imprint of coccolithophore morphological evolution on carbonate production and burial.

MDI as a recorder of long-term seasonal modulations

We posit that the MDI index responds to variations in the amplitude of tropical seasonality. In low latitudes, seasonal contrast is related to the eccentricity of Earth's orbit[23,31], 1) directly because the ellipticity of the orbit determines the distance between the Sun and the Earth during each season, affecting radiation intensity, and 2) indirectly because eccentricity modulates the effect of precession on seasonal insolation contrast. Seasonal contrast is greater during periods of high eccentricity. To our knowledge, the eccentricity-paced rhythm of surface-ocean seasonality that dominates MDI has not been documented previously because most proxies record integrated annual average conditions or a specific season. In the modern inter-tropical ocean, large seasonal changes in upper water column properties (e.g., mixed-layer depth, nutrient availability) are associated with the seasonally-reversing monsoon systems and latitudinal migrations in the inter-tropical convergence zone. The seasonal succession of coccolithophore species, a characteristic of phytoplankton ecology, is indicative of their adaptation to the different ecological niches created by seasons[24]. In the modern ocean, highest phytoplankton diversity is found in the tropical band, a pattern probably related to high temperatures and stable conditions, whereas seasonal species turnover is highest at mid-latitudes because of a strong seasonal temperature contrast[32]. Intra-annual dynamics of Net Primary Production (NPP) are good descriptors of the range of oceanographic niches and biomes[25], because NPP represents the integrated biological response to all of the changes forced by the ocean-atmosphere coupled system. To demonstrate the effect of orbital configuration on NPP seasonality and therefore niche availability, we simulate monthly oceanic NPP using the IPSL-CM5A-2 model[6]coupled ocean with PISCES-V2 biogeochemical model[5], for seven early Pleistocene time intervals covering a large eccentricity spectrum with different precession conditions but with similar ice volume and obliquity (Extended Data Table 3, Fig. 1b). The results of these simulations for the tropical Indian and western Pacific Oceans show that the seasonal range of NPP increases with eccentricity, a trend that parallels the eccentricity sorted values of MDI in our Plio-Pleistocene time series (Fig. 3).

In the simulations, the increase in amplitude of the NPP seasonal cycle (Fig. 3a and Extended Data Figure 4a-e) is primarily driven by higher productivity during boreal summer, especially in the eastern Indian ocean. This increase is forced by modification of atmosphere-ocean dynamics in response to variations in the amplitude and seasonality of insolation forcing (Extended Data Fig. 5a-c). Eccentricity acts on sea-level pressure over continental Asia (Extended Data Fig. 5d-h) via insolation, inducing modifications of sea-level pressure gradients and low-level wind circulation over the Indo-Pacific Warm Pool, IPWP (Extended Data Fig. 4f-h). Changes in atmospheric dynamics are responsible for regional and seasonal enhancement of NPP at high eccentricity (Extended Data Fig. 4a-c), either via generation of anomalous upwelling along the equator (SW of India) or modification of the hydrological cycle that create more favorable conditions for intense vertical mixing (Extended Data Fig. 6a and c), depending on precession. Overall, those localised increases in the amplitude of the seasonal cycle lead to a less homogeneous upper ocean in the IPWP region at high eccentricity (Fig. 3a, Extended Data Fig. 4a-c). We propose that during high eccentricity times, the higher seasonal range of NPP in our model simulations (representing up to 100% of mean annual NPP) is indicative of more diverse ecological niches that coccolithophores can adapt to. A greater diversity of ecological niches when seasonality is high[25] leads to a larger number of species because Noelaerhabdaceae adaptation is characterised by the adjustment of coccolith size and degree of calcification to thrive in the new environments[1,2]. Exact core locations in Figure 3a are not relevant, as recorded evolutionary events may have originated anywhere in the tropics.

Eccentricity lags, species origination, and dominance

Coccolith morphological diversity clearly responds to eccentricity (Fig. 1); however, in stark contrast to Plio-Pleistocene climate proxy records[22,33] and coccolithophore assemblage dynamics[16-18], precession and obliquity cycles are absent from the 2 kyr resolution MDI records (Extended Data Figure 2b-j). Those cycles could have been smoothed our by an adaptive strategy acting as a lowpass filter. This would explain the phase shift observed between eccentricity and Noelaerhabdaceae morphology (Fig. 1b, Extended Data Fig. 2a; Extended Data Fig. 2a). Speciation events spread rapidly throughout the oceans[19,21], and species dominance takes more time , as shown by the history of *Emiliania huxleyi*: it appeared at 290 ka, but did not become dominant until 90 ka[19], at time of an intense low-eccentricity interval (Extended Data Figure 7). It was not until two e100 cycles later that *E. huxleyi* gained a competitive advantage and rose to dominance over G.oceanica and G. ericsonii. The delay between species appearance and dominance, intrinsic is smoothing out the variability at precession and obliquity timescales in the MDI record (Fig. 1b, Extended Data Fig. 7). The eccentricity lags and transfer of spectral power from high to low frequencies described here are analogous to modelling results in a recent study of deep-time carbon cycle variations on orbital timescales[34], hinting that coccolithophores may drive, rather than just respond to, carbon cycle changes.

Long-eccentricity forcing, coccolithophores, and the global carbon cycle

The persistence of e100 and e405 cycles in Cenozoic and Mesozoic records of the ocean carbon cycle (e.g., percent $CaCO_3$ and foraminiferal $\delta^{13}C$), independent of glacial-interglacial climate state, attests to the importance of biogeochemical processes operating at these timescales throughout Earth's history [e.g.,35,36]. For examples, during the Pleistocene Mediterranean surface $\delta^{13}C$ records document e405 cycles more faithfully than deep open-ocean records, suggesting a low-latitude origin of this signal[28]. Chemical weathering has been suggested as a potential modulator of the ocean carbon cycle on 400-kyr timescales[37]. Similar to our coccolith records, a significant phase lag between $\delta^{13}C$ and eccentricity is observed in the e405 band, which has been explained by the long residence time of carbon in the oceans and resultant transfer of energy from precession into eccentricity bands via a non-linear process[34,35]. Previously, coccolith records spanning up to ~1 Myr have linked to eccentricity forcing of productivity[17,27]. Yet changes reconstructed at our low-latitude sites cannot be explained by the hypothesis that eccentricity-driven changes in growing season length are responsible for the ~400-kyr cycle in coccolithophore production[27]. Our data and model results support the alternative hypothesis that changes in seasonality caused by the eccentricity of the Earth's orbit paced tropical Noelaerhabdaceae evolution and production throughout the Pleistocene. Although these changes clearly impact carbonate accumulation patterns (Fig. 1g), coccolithophore productivity alone cannot be responsible for the expression of long eccentricity cycles in climate records because they are only one constituent of the phytoplankton. Other phytoplankton groups, some with little or no fossil record, may also have been similarly influenced by variations in tropical seasonality on these timescales. In this case, the impact of changes in the ratio of exported organic carbon production to carbonate mineral production, known as the rain ratio[38], may have been strong enough to modulate the carbon cycle. The cyclic evolution of calcifying phytoplankton on eccentricity timescales in response to seasonality documented here, support the hypothesis that biosphere productivity must have responded to changes in solar insolation[35,37] thus explaining the strong e405 signature in carbon cycle records.

Main references

1 Beaufort, L. *et al.* Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. *Nature* **476**, 80-84, doi:10.1038/nature10295. (2011).

2 Henderiks, J. & Bollmann, J. The *Gephyrocapsa* sea surface palaeothermometer put to the test: comparison with alkenone and foraminifera proxies off NW Africa. *Mar. Micropaleontol.* **50**, 161-184 (2004).

3 Bendif, E. M. *et al.* Repeated species radiations in the recent evolution of the key marine phytoplankton lineage Gephyrocapsa. *Nature Communications* **10**, 4234, doi:10.1038/s41467-019-12169-7 (2019).

4 Ruddiman, W. F. & Raymo, M. E. in *The past three million years : Evolution of climatic variability in the North Atlantic Region* (eds N.J. Shackleton, R.G. West, & D.Q Bowen) (University Press, 1988).

5 Sepulchre, P. *et al.* IPSL-CM5A2 – an Earth system model designed for multi-millennial climate simulations. *Geosci. Model Dev.* **13**, 3011-3053, doi:10.5194/gmd-13-3011-2020 (2020).

6 Aumont, O., Éthé, C., Tagliabue, A., Bopp, L. & Gehlen, M. PISCES-v2: An ocean biogeochemical model for carbon and ecosystem studies. *Geoscientific Model Development Discussions* **8** (2015).

7 Broecker, W. & Clark, E. Ratio of coccolith CaCO3 to foraminifera CaCO3 in late Holocene deep sea sediments. *Paleoceanography* **24** (2009).

8 Suchéras-Marx, B. *et al.* The colonization of the oceans by calcifying pelagic algae. (2019).

9 Ridgwell, A. & Zeebe, R. E. The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth and Planetary Science Letters* **234**, 299-315 (2005).

10 Young, J. *et al.* A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue* **1**, 1-132 (2003).

11 Henderiks, J. Coccolithophore size rules—reconstructing ancient cell geometry and cellular calcite quota from fossil coccoliths. *Mar. Micropaleontol.* **67**, 143-154 (2008).

12 Filatov, D. A. Extreme Lewontin's paradox in ubiquitous marine phytoplankton species. *Molecular Biology and Evolution* **36**, 4-14 (2019).

13 Bown, P. R. Calcareous nannoplankton evolution: a tale of two oceans. *Micropaleontology* **51**, 299-308 (2005).

14 Si, W. & Rosenthal, Y. Reduced continental weathering and marine calcification linked to late Neogene decline in atmospheric CO2. *Nature Geoscience* **12**, 833-838, doi:10.1038/s41561-019-0450-3 (2019).

15 Bolton, C. T. *et al.* Decrease in coccolithophore calcification and CO 2 since the middle Miocene. *Nature communications* **7**, 1-13 (2016).

16 Gibbs, S. J., Shackleton, N. & Young, J. Orbitally forced climate signals in mid-Pliocene nannofossil assemblages. *Mar. Micropaleontol.* **51**, 39-56 (2004).

17 Beaufort, L. *et al.* Insolation Cycles as a Major Control of Equatorial Indian Ocean Primary Production. *Science* **278**, 1451-1454 (1997).

18 Chepstow-Lusty, A., Backman, J. & Shackleton, N. J. in *Ruddiman, WF, Sarnthein, M., et al., Proc. ODP, Sci. Results.* 121-141.

19 Thierstein, H. R., Geitzenauer, K. R., Molfino B. & Shackleton, N. J. Global synchroneity of late Quaternary coccolith datum levels : validation by oxygen isotopes. *Geology* **5**, 400-404 (1977).

20 Bollmann, J., Baumann, K. H. & Thierstein, H. R. Global dominance of Gephyrocapsa coccoliths in the Late Pleistocene: Selective dissolution, evolution, or global environmental change? *Paleoceanography* **13**, 517-529, doi:10.1029/98PA00610 (1998).

21 Raffi, I. *et al.* A review of calcareous nannofossil astrobiochronology encompassing the past 25 million years. *Quaternary Science Reviews* **25**, 3113-3137, doi:https://doi.org/10.1016/j.quascirev.2006.07.007 (2006).

22 Lisiecki, L. E. & Raymo, M. E. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography* **20**, doi:10.1029/2004PA001071 (2005).

23 Laskar, J. *et al.* A long-term numerical solution for the insolation quantities of the Earth. *Astronomy & Astrophysics* **428**, 261-285, doi:10.1051/0004-6361:20041335 (2004).

24 Okada, H. & McIntyre, A. Seasonal distribution of modern Coccolithophorees in the western north Atlantic ocean. *Marine Biology* **54**, 319-328 (1979).

25 Longhurst, A. *Ecological Geography of the Sea*. Vol. 1 (Academic Press, 1998).

26 Sexton, P. F. & Barker, S. Onset of 'Pacific-style' deep-sea sedimentary carbonate cycles at the mid-Pleistocene transition. *Earth and Planetary Science Letters* **321-322**, 81-94, doi:https://doi.org/10.1016/j.epsl.2011.12.043 (2012).

27 Rickaby, R. E. M. *et al.* Coccolith chemistry reveals secular variations in the global ocean carbon cycle? *Earth and Planetary Science Letters* **253**, 83-95 (2007).

28 Wang, P., Tian, J. & Lourens, L. J. Obscuring of long eccentricity cyclicity in Pleistocene oceanic carbon isotope records. *Earth and Planetary Science Letters* **290**, 319-330, doi:https://doi.org/10.1016/j.epsl.2009.12.028 (2010).

29 Suchéras-Marx, B. & Henderiks, J. Downsizing the pelagic carbonate factory: Impacts of calcareous nannoplankton evolution on carbonate burial over the past 17 million years. *Global and Planetary Change* **123**, 97-109, doi:https://doi.org/10.1016/j.gloplacha.2014.10.015 (2014).

30 Holligan, P. M. *et al.* A biogeochemical study of the coccolithophore, Emiliania huxleyi, in the North Atlantic. *Global Biogeochemical cycles* **7**, 879-900 (1993).

31 Laepple, T. & Lohmann, G. Seasonal cycle as template for climate variability on astronomical timescales. *Paleoceanography* **24** (2009).

32 Righetti, D., Vogt, M., Gruber, N., Psomas, A. & Zimmermann, N. E. Global pattern of phytoplankton diversity driven by temperature and environmental variability. *Science Advances* **5**, eaau6253, doi:10.1126/sciadv.aau6253 (2019).

33 Ruddiman, W. F., Raymo, M. & McIntyre, A. Matuyama 41,000-year cycles : North Atlantic Ocean and Northern hemisphere ice sheets. *Earth Plan. Sci. Lett.* **80**, 117-129 (1986).

34 Zeebe, R. E., Westerhold, T., Littler, K. & Zachos, J. C. Orbital forcing of the Paleocene and Eocene carbon cycle. *Paleoceanography* **32**, 440-465 (2017).

35 Pälike, H. *et al.* The Heartbeat of the Oligocene Climate System. *Science* **314**, 1894-1898, doi:10.1126/science.1133822 (2006).

36 Herbert, T. D. A long marine history of carbon cycle modulation by orbital-climatic changes. *Proceedings of the National Academy of Sciences* **94**, 8362-8369 (1997).

37 Ma, W., Tian, J., Li, Q. & Wang, P. Simulation of long eccentricity (400- kyr) cycle in ocean carbon reservoir during Miocene Climate Optimum: Weathering and nutrient response to orbital change. *Geophysical Research Letters* **38** (2011).

38 Archer, D. & Maier-Reimer, E. Effect of deep-sea sedimentary calcite preservation on atmospheric CO2 concentration. *Nature* **367**, 260-263 (1994).

Figure legends

Figure 1: Noelaerhabdaceae coccolith morphology and accumulation, eccentricity, and climate over the last 2.8 million years. a: Frequency contour plot of multi-site stacked coccolith length (see Methods). Scanning electron microscope images represent examples of the diversity of Noelaerhabdaceae morphologies over time. 1: *Emiliania huxleyi*, 2: *Gephyrocapsa ericsonii*, 3: *G. oceanica*, 4: *G. caribbeanica*, 5-6: *G. omega*, 7- 8: mid-size *Gephyrocapsa*, 9: small *Gephyrocapsa*, 10: *Pseudemiliania ovata*, 11: *Reticulofenestra minuta*, 12: left: *P. ovata*, right: *R. minutula*. **b**: Mean coccolith length in the multi-site stack (blue), plotted with Earth's eccentricity[23] (dotted black line) and low-pass filtered eccentricity with an angular frequency of 0.021 kyr^{-1} (red). Described Noelaerhabdaceae acmes[19-21] are shown as black bars (*I* = *E. huxleyi*; *II*= *G. caribbeanica*; *III* and *IV* = mid-size *Gephyrocapsa*). Coloured stars and diamonds on the eccentricity curve show the timing of actual orbital configurations used in model simulations (Pmax = perihelion in December, Pmin = perihelion in June); smaller grey symbols indicate times throughout the record with similar eccentricity and precession configurations to those modelled (see Methods). **c**: LR04 benthic foraminiferal $\delta^{18}O$ stack [22]. Grey band illustrates the small range of benthic $\delta^{18}O$ between model simulations. **d**: Evolutive cross-spectral analysis between MDI and eccentricity (see Methods). Colour-scale shows coherency (90% Confidence Level (CL) above 0.7); Horizontal dashed lines show eccentricity periods. **d'**: MTM spectral analysis of detrended MDI stack. Shaded areas are above the CL90% (dashed line). Solid black line is

CL95%. **e**: MDI Stack (2 kyr resolution, see Methods). **f**: Evolutive cross-spectral analysis between NoMAR and MDI (CLs as in d). **f'**: MTM spectral analysis of detrended NoMAR stack. CLs as in d'. **g**: NoMAR stack (2 kyr resolution, see Methods). MDI and NoMAR stacks are smoothed with a Loess function, and blue shading shows maximum and minimum values across all records.

Figure 2: Morphological Divergence Index (MDI) concept. a: Schematic representation of the MDI. Here we consider an evolutionary sequence with three successive epochs of a species A (Epoch 1) of intermediate morphology evolving into 2 species, B (smaller) and C (larger). In Epoch 2, B and C have equivalent proportions in the population, and in Epoch 3, they fluctuate in relative abundance between 25% and 75%. The evolutionary event between Epoch 1 and 2 (red shading) is not detected in the mean population morphology (e.g., size, mass). In Epoch 3, fluctuating ecology produces population dynamics detected in mean morphology (grey shading). With a biometric boundary fixed at 2 units, MDI will jump from 0 to 2 units from Epoch 1 to 2, showing that it is diagnostic of an evolutionary sequence. In Epoch 3, MDI remains stable despite fluctuating assemblage composition. In this idealised example, average population biometry is related to ecology and MDI to evolution. **b**: MDI calculated for core IODP Site U1485. **b3**: average Noelaerhabdaceae coccolith mass (smoothed using a Loess function). **b2**: two size classes are created: coccoliths shorter and longer than 3 µm (grey histograms). MDI is the difference between the average log(mass) of each class (light and dark grey dots on histograms). Thus, MDI can differ substantially from average coccolith mass (black dots on mass distribution plots), and two samples can have a similar MDI but very different average mass and mass distributions (e.g., 180 ka vs 190 ka), or very different MDI but similar averages (e.g., 3 ka vs 190 ka). In this way, MDI isolates morphological variability resulting from evolutionary changes in the number of different

morphotypes present within the population. **b1**: MDI record (identical Loess smoothing window as in **b3**). Different smoothed curves illustrate the effect of different length or mass thresholds used to calculate MDI: solid red line = 3 µm, red dotted line = 2.7 µm, red dashed line = 3.6 µm, solid blue line = 3.16 pg.

Figure 3: Modelled NPP seasonal contrast under different eccentricity configurations and morphological divergence index. a: Eccentricity-driven changes in the seasonality of net primary production (NPP) in the tropical Indo-Pacific. Colour scale shows the vertically integrated NPP seasonal contrast difference between numerical model outputs computed at maximum and minimum eccentricity, each run at perihelion in June (Pmin) and December (Pmax) and then averaged (Methods) (i.e., Seasonality E_{max}− Seasonality E_{min}). Values are expressed as a percentage of mean annual pre-industrial NPP simulated in reference 5. Red (blue) colours imply higher seasonality at high (low) eccentricity. Black circles show sediment core site locations used in this study: 1: IODP U1446; 2: IODP U1448; 3: IODP U1443; 4: MD97-2140; 5: MD05-2920; 6: IODP U1486; 7: IODP U1485; 8: MD05-2930; 9: IODP U1483 (Extended Data Table 1). **b**: Box-whiskers plot of all MDI values, sorted and binned by increasing low-pass filtered eccentricity, compared to the seasonal contrast of NPP (maximum minus minimum month) from seven numerical simulations (see Methods). Model points represent a regional mean of the entire map area. As in Fig. 1b, orange diamonds are model runs with perihelion in December (Pmax: 2222 ka, 2265 ka, and 2380 ka), green stars are runs with perihelion in June (Pmin: 2230 ka, 2346 ka, 2369 ka, and 2395 ka) – illustrating that eccentricity has a much larger effect on seasonality than precession at a given eccentricity.

Methods

Coccolith data acquisition

Over eight thousand samples were extracted from sediment cores for coccolithophore analysis at depth intervals to achieve a high stratigraphic resolution (0.5 to 2.3 kyr, Extended Data Table 1). Samples were prepared using the settling method[39,40]: sediments were disaggregated in water and suspensions were settled onto a 12x12 mm cover slip and mounted with Norland Optical Adhesive 74, with 8 cover slips per microscope slide. Some samples were prepared as independent duplicates. Two slides (16 samples) were placed onto the stage of an automated polarizing microscope (Leica DM6000). Following auto-focusing, 165 contiguous fields of view (with an area of 125 x 125 µm each) were imaged in each sample using a black and white SPOTFLEX camera (Diagnostic Instrument). SYRACO, a software program based on an Artificial Neural Network[41], identified all specimens belonging to 33 groups of coccolithophore taxa in the images[42]. The gephyrocapsid specimens, the dominant group studied here, were classified into six distinct classes that were merged into one group. On average, 888 Noelaerhabdaceae coccoliths were identified in each sample. Among other morphometric parameters, size and mass of the coccoliths were measured. Coccolith mass is measured using birefringence, following published state-of-the-art methods[40,43]. The use of Artificial Intelligence in this type of work is essential because it is the only way to measure such a large number of specimens (>7 million) in a reasonable time, and thus obtain the high-resolution multi-site records required for this study.

The pattern recognition was performed with a structured multi-layer neural network called SYRACO, written in C++ by D. Dollfus[44]. The input image of 64x64 pixels is connected to the output (class name) by three convolutional layers of 1764, 360 and 80 neurons with no shared weights, which induces long computing time. The advantages of this structure are discussed in reference 45. In order to mimic the dynamic process of human recognition, in parallel to the second and third convolutional layers, there are three small neural networks of 20 neurons each, called motor layers that perform simple image transformations from five possibilities: rotation, translation, symmetry, contrast, and dilation. These parallel neural networks enhance the efficiency of the pattern recognition by 50%[41] with an accuracy above 95% (based on >5000 test images). In his PhD thesis, Barbarin[42] increased the number of calcareous nannofossil species recognised by SYRACO to include most Cenozoic species and grouped them into 49 morphological classes. The number of false positives (non-coccolith particles of calcareous debris such as broken foraminifera, micrite, broken coccoliths) has been reduced in SYRACO by adding a second pattern recognition level after the SYRACO Artificial Neural Network (ANN), based on a Random Forest algorithm[46]. This cross-checking is more robust because it results in only 5% of false positives, compared to ~50% before[42]. In this work, we combine the 49 morphological classes into only five groups and work essentially with one of these, the Noelaerhabdaceae. From the confusion matrix produced by the analysis of 6888 images (ref. 42, Table 1, p.109), the percentage of successful identifications for those five taxonomic groups are 96% for Noelaerhabdaceae; 91% for Coccolithales; 90% for Syracosphaearales and Zygodiscales (grouped together); and 88% for other coccolith taxa. *Florisphaera profunda* coccoliths are recognised at a rate of 98%[42]. Most of the losses can be explained by the quality of the captured image due to some particle in a large image being out of focus or luminosity and contrast problems, or aggregation of particles. We progressively solved some of these problems by developing new optical methods[40,43] and by changing the pre-processing (e.g., refining image segmentation); this increased the number of recognized coccoliths without changing the proportion of the different species. Because we were satisfied with its performance, we did not test other architectures of SYRACO such as increasing the number and the size of the convolutional layers. The goal of SYRACO was to provide a robust and rapid coccolith extractor compatible with commercial computer performance during development in the late 1990s and early 2000s. In this work, SYRACO was processed on a Dell Precision T7910 with 2 Xeon processors (2.3 GHz) of 20 cores each and 64 Go of memory, with Windows as the operating system.

Site-specific chronologies

IMAGES core MD97-2140[47] : The age model for Site MD97-2140[47], on the Eauripik Rise in the Western Pacific Warm Pool, is based on tuning of a high-resolution planktonic foraminiferal *Globigeronoides ruber* $\delta^{18}O$ record to the astronomically calibrated ODP Site 677 $\delta^{18}O$ *G. ruber* record[48], located in the eastern equatorial Pacific. This age model yields a chronology consistent with major micropaleontological (disappearance of *G. ruber* pink variety) and palaeomagnetic (Brunhes–Matuyama boundary) events[49].

IMAGES core MD05-2920[50] :The age model for Site MD05-2920[51], on the southern bank of Manus Island, is based on ten Accelerator Mass Spectrometer (AMS) ^{14}C dates obtained from the surface-dwelling planktonic foraminifera *G. ruber* (white), and a correlation between the benthic foraminiferal $\delta^{18}O$ record and the reference LR04 benthic foraminiferal $\delta^{18}O$ stack[22].

IMAGES core MD05-2930[50] :The age model for Site MD05-2930[52], in the Coral Sea, is based on ten AMS ^{14}C measurements of *G. ruber sensu stricto* (*ss*), and on correlation of the MD05-2930 $\delta^{18}O$ *G. ruber* ss record with the LR04 benthic foraminiferal $\delta^{18}O$ stack[22].

IODP Site U1443[53] : The age model for Site U1443, on the Ninetyeast Ridge in the southernmost Bay of Bengal, is based on correlation of physical properties data on the primary shipboard splice to the LR04 benthic foraminiferal $\delta^{18}O$ stack[22]. Physical properties were measured onboard the RV *Joides Resolution* on archive halves from all holes at Site U1443, and correlation and splicing were based on magnetic susceptibility, natural gamma ray, and reflectance spectroscopy b* data[54].

IODP Site U1448[53] : The age model for Site U1448, in the Andaman Sea, is based on correlation of the Site U1448 Ti/Ca record, derived by X-Ray Fluorescence (XRF) core scanning, to the XRF Ti/Ca record of Indian National Gas Hydrate Program (NGHP) Site 17 – a very close site with age control based on a benthic foraminiferal oxygen isotope record tuned to the LR04 benthic foraminiferal $\delta^{18}O$ stack[22,55,56].

IODP Site U1446[53] : The age model for Mahanadi Basin Site U1446 is based on correlation of a high-resolution benthic foraminiferal oxygen isotope stratigraphy to the LR04 benthic foraminiferal $\delta^{18}O$ stack[22,57].

IODP Site U1483[58]: The age model for Scott Plateau Site U1483 is based on the shipboard integrated magneto-biostratigraphy, and on correlation of the U1483 L* record, which presents strong G-IG variability, to the LR04 benthic foraminiferal $\delta^{18}O$ stack[22].

IODP Site U1485[58]: The age model of the northern Papua Margin Site U1485 is based on correlation between the benthic foraminiferal $\delta^{18}O$ record of this site and the LR04 benthic foraminiferal $\delta^{18}O$ stack[22].

IODP Site U1486[58]: The age model of the upper 100 m (the last 1.6 Ma) of Site U1486, from the southern bank of Manus Island, is based on a correlation between the benthic foraminiferal $\delta^{18}O$ record and the LR04 benthic foraminiferal $\delta^{18}O$ stack[22]. Below 100 m, the age model is based on the shipboard integrated magneto-biostratigraphy and correlation of the U1486 L* record (that shows strong G/IG variability) with the LR04 benthic foraminiferal $\delta^{18}O$ stack[22].

Construction of composite frequency contour plot of coccolith size

Measurements were grouped into morphological bins of 0.1 μm for coccolith length in every sample. Samples were binned into 30-kyr time windows in each core, chosen such that it is larger than the length of a precession cycle (23-19 kyr). This will prevent any bias in the size/mass distribution resulting from changes in the relative abundance of large versus small gephyrocapsid species on precessional timescales[59]. Another advantage of using a 30-kyr time window is that the high number of measurements included in each bin (on average 16650 measurements) make it extremely precise but easier to discern trends. To standardise each time window at each site, the numbers contained in each bin are divided by the total number of coccoliths in that time window and multiplied by 100. To stack the records and produce the frequency-density plot of size (Fig. 1a), samples in each core were grouped into 30 kyr bins, standardised (%) and merged into a single stack. Frequency contour plots for size and mass (latter not shown) show near-identical trends and variability. The distribution of coccolith mass values is skewed toward heavy values. We therefore used the logarithm of the mass to obtain a symmetrical mass distribution before binning (0.05 log(pg) bins) and stacking as for length.

Note on taxonomy of the Pleistocene Noelaerhabdaceae:

The genus concept in the Pleistocene Noelaerhabdaceae is rather straightforward[10,60]: *Emiliania* presents “T-shaped” elements in its distal shield, *Gephyrocapsa* presents a bridge in its central area, *Pseudoemiliania* presents slits in its distal shield and *Reticulofenestra* has none of these features. Two of these features may be present on *Gephyrocapsa* (e.g. *G. protohuxleyi*). The species concept is much more complex[10,60,61]. It essentially depends on coccolith size, ratio of central area opening to coccolith size, and bridge angle (for *Gephyrocapsa*). All these features are continuous rather than discrete parameters and therefore often present a continuum between species. In Fig. 1a and b, the size density plot and the average size plot illustrate how size is a variable feature. One of the main taxonomic parameters of this group (i.e., size) is constantly evolving, complicating the common use of a size-based typological species concept. *Bendif et al.*[3] indicate that all extant species evolved from *Gephyrocapsa caribbeanica* around 550 000 years ago, implying a rapid (<0.55 Myr) species turnover. The Noelaerhabdaceae family is therefore rapidly evolving genetically and morphologically. In this paper we do not intend to dispute taxonomy or species concepts. Given that it is difficult to follow genetic and typological species through time in this family, we prefer to discuss morphological evolution in a taxon-free manner. In the described taxonomies of this family[60], there remains however a clear cut-off between smaller and larger Noelaerhabdaceae species' coccoliths around 3 μm, which is why we choose this boundary to develop the MDI concept.

Morphological Divergence Index (MDI)

To quantitively capture the history of biological evolution within a group of species with a biometric tool, it is necessary to build a metric that it is as independent as possible from the population dynamics of the different species relative to the others. This is because the biometry of a multi-species population is greatly influenced by its population dynamics: the relative success of one species in one particular biotope will affect the average biometry of the entire population. The average biometry is therefore greatly influenced by species adaptation to biotopes and will not be necessarily diagnostic of biological evolution. A way to limit the influence of the relative abundance of species in a sample is to measure the difference between the biometric means of the considered species. A simple index can be designed to parametrize a biometric boundary between two populations: the arithmetic distance between the two population means. A schematic example of an evolutionary sequence as recorded by MDI is described in Figure 2a.

Therefore, the MDI is *not* designed: (1) to trace the spatial variation of ecological parameters such as seasonality. This is because a new morphological trait will spread rapidly (on geological timescales) in the ocean if it is successful. The MDI will be distributed evenly wherever the species are present, or (2) to describe a physiological adaptation to a fluctuating environment.

MDI *is* designed (1) to trace the morphologic evolution of a small group of species. (2) to trace temporal variations of ecological parameters at the large geographical scale that can lead to the evolution of new morphological traits.

MDI designed for Plio-Pleistocene Noelaerhabdaceae

In each sample, individual coccoliths were divided into two size classes: coccoliths longer and shorter than 3 µm. The average log(mass) is calculated in both classes. MDI is the difference between the two averages (Fig. 2b). The size of 3 µm corresponds to the best cut-off value between the two modes (2.8 and 3.9 µm) of the size distribution. Other size cut-offs (2.9, 3.25 and 3.5 µm) as well as a mass cut-off (3.16 pg) were tested, without large differences in the resulting MDI values and temporal trends (see Fig. 2b). The records are resampled (by linear integration) at 2 kyr intervals for further analysis (time series, statistics, and stacking). A stacked record composed of all records is calculated for each time window. This stacked MDI reflects the variability seen in all individual records (Extended Data Figure 1). Because not all records cover the entire 2.8 Myr interval (3 records are over 2.3 Myr long, 3 are between 0.7 and 1.8 Myr long, and 3 are 0.4-0.6 Myr long), the stack is composed of more records in the younger part than in the older part. Because of the phase lag between MDI and eccentricity we use band-passed eccentricity (red line in Fig. 1b) to sort and bin MDI values used for Figure 3b. Finally, because the relative abundances of small versus larger Noelaerhabdaceae are not considered during the calculation of the MDI, any preferential dissolution of smaller more fragile coccoliths would not affect the MDI, as it represents the difference between the mean masses of the two size groups. A negligible effect of carbonate dissolution on MDI is supported by the fact that species-specific mean coccolith mass is conserved in dissolution experiments[62], and by the similarity between MDI records regardless of core depth in the range ~1100-3000 m (all well above the Pleistocene Pacific carbonate saturation horizon) (Extended Data Figure 1).

Mass accumulation rates

Mass accumulation rates of Noelaerhabdaceae coccoliths (NoMAR) were estimated in seven cores (all cores excluding MD05-2530 and U1446) for which a quantitative sample preparation techniques was applied[40]: The samples were prepared by settling onto coverslips that were weighed before and after settling, the weight difference providing the amount of sediment deposited. The number and the mass of the Noelaerhabdaceae is estimated by SYRACO. From these quantities it is possible to estimate the weight of Noelaerhabdaceae per gram of sediment. NoMAR is obtained by multiplying weight per gram by the sedimentation rate and the dry bulk density of sediment. The dry bulk density was estimated from continuous measurements of wet bulk density from gamma ray attenuation (GRA) and transformed by the linear relationship for each site between discrete shipboard measurements of wet bulk density and dry bulk density[63]. NoMARs for the 7 cores were stacked together after resampling each record at 2 kyr intervals (Fig 1g), using the same method as for MDI. Other stacking methods, such as assembling loess-detrended records, were tried and produced consistent results. Differences exist between individual NoMAR records due to regional difference in coccolithophore productivity, export dynamics, and core depth (although only 2 cores, MD97-2140 and U1443, were retrieved from sediments deeper than 2000 m). However, three common patterns emerge in all individual records: an increasing trend in NoMAR towards the present, a stepwise increase at ~1.1 Ma, and the clear presence of eccentricity cycles. Noelaerhabdaceae coccolith flux (Extended Data Fig. 3b) is calculated as the number of coccoliths per gram of sediment multiplied by the sedimentation rate, and is the main driver of the step increase in NoMAR at ~1.1 Ma.

Time series analysis

Time series analyses were performed using the software packages Analyseries[64] and Acycle[65] on detrended records. Cross-spectral analyses were performed in Analyseries using Blackman-Turkey transforms[66]. For evolutive cross-spectral analyses (Fig. 1d, f) a window of 500 kyr (250 data points) and a step of 100 kyr was used. Coherence values above 0.56 are above the 80% confidence level. Spectral Analyses were performed with the Multi Taper Method (MTM)[67] with both evolutive and entire series (Extended Data Fig. 2). Spectral properties are similar in all individual MDI records, and show that the absence of precession (19-23 kyr) and obliquity (~41 kyr) is not a result of chronological bias in constructing the stack that would have smoothed the record. Each record has a ~2 kyr resolution with a precise independent age model. The absence of precession and obliquity is therefore a common and robust feature of all of the MDI series as well as the stacked record.

Low-pass filters

We designed 2nd order low-pass filters in order to reproduce the effect of the time needed for a new evolved species to fully succeed (200 kyr for *E. huxleyi*). We transformed the following classical low-pass filter complex transfer function *H*:

$$H(j\omega) = \frac{A}{1+\frac{j\,\omega}{Q\omega_0}-\frac{\omega}{\omega_0}^2}$$

(where A is the amplitude, Q is the quality factor, ω is the angular frequency $2\pi f$, (f the frequency)) in its associated differential equation:

$\frac{d^2y}{dt^2} + \frac{\omega_0}{Q}\frac{dy}{dt} + \omega_0^2 y = \omega_0^2 x$ where y is the output series and x the input series.

We solved it numerically as follow:

$$y_t = \frac{1}{1+\frac{\omega_0}{Q}+\omega_0^2}((2+\omega_0)y_{t-1} - y_{t-2})A\omega_0^2 x_t$$

Two configurations have been chosen: one produces a delay of 200 kyr for the new species' success, the second produces a delay of 130 kyr (Extended Data Figure 8a). To obtain those delays, we used the following values:

First case (delay of 200 kyr), ω_0 = 0.021, Q = 1, A = 1

Second case (delay of 130 kyr), ω_0 = 0.035, Q = 1.02, A = 0.65

The delay of 200 kyr corresponds to the time between the First Appearance Datum (FAD) and the beginning of the acme (BA) of *E. huxleyi*[21]. The FAD of this species is well documented because its characteristic T shape elements are a morphological feature that appeared suddenly, without gradation. The other *Gephyrocapsa* species have been described using criteria that are subject to gradation between species: coccolith length, size of the central opening, and orientation of the bridge[68]. For example, the FAD of a typical *G. ericsonii*, (a small gephyrocapsid) that appeared at about the same time as *E. huxleyi*[3] is not reported precisely because it evolved progressively from *G. caribbeanica* (a mid-size species). It is interesting to note that the FAD and the BA of *E. huxleyi* occurred similarly in times of eccentricity decrease, but two cycles apart. The intermediate cycle may have been too high to allow *E. huxleyi* to begin its dominance. This may not have been the case for other species under different orbital configurations. This is why we did a filter with a different configuration, which produces a delay of about one eccentricity cycle between a FAD and a BA. In order to express the response of those filters, we built their Bode magnitude plots, expressing the frequency response, and their Bode phase plots, expressing the phase shift (Extended Data Figure 8b, c).

Model Description

To simulate changes in Net Primary Production (NPP) related to changes in eccentricity we used the Earth System Model IPSL-CM5A2[5] that simulates the interactions between ocean, atmosphere, land and ice. The following section provides a brief description of model components and experiments setup. We then describe the model behaviour at low eccentricity and discuss how the large-scale ocean-atmosphere circulation at high eccentricity in our simulations compare to previous modelling studies.

The IPSL-CM5A2 coupled model is a combination of the LMDz5A atmospheric model[69], the ORCHIDEE[70] land surface model and the NEMOv3.6 oceanic model[71]. The NEMO model includes an ocean dynamic component (OPA[72]), a sea-ice thermodynamics model (LIM2[73]) as well as a biogeochemistry model (PISCES-v2[6]) and has an horizontal resolution of 2° by 2° (refined to 0.5° in the tropics) and 31 vertical levels, whose thickness increases from 10 m at the surface to 500 m at the bottom. The atmospheric grid has a horizontal resolution of 1.875° in latitude by 3.75° in longitude with 39 vertical levels. The ocean-atmosphere coupling is ensured by the OASIS coupler[74] that interpolates and exchanges variables between the two components. Detailed description of IPSL-CM5A2 and performances in simulating pre-industrial climate can be found in references [5,75]. PISCES-v2 simulates the main oceanic biogeochemical cycles (C, P, Si, N and Fe) and has a simple representation of the lower trophic levels of the marine ecosystem[6], with two phytoplankton (nannophytoplankton and diatoms) and two zooplankton (micro- and meso-zooplankton) size classes and five limiting nutrients (Fe, NO_3^-, NH_4^+, Si and PO_4^{3-}). Phytoplankton growth is controlled by nutrients, light availability, and water temperature. In the version of the model we used, river supply to the ocean of all elements apart from DIC and alkalinity is taken from the GLOBAL-NEWS2 data sets[76] and does not vary from one simulation to another. Model parameterizations are detailed in reference 6.

Simulations were performed for seven early Pleistocene time slices and differ only by their respective orbital parameters (Extended Data Table 3, Figure 1b). The time slices were chosen in order to target the signal produced by the 405-kyr eccentricity cycle. Land-sea mask, ice-sheets configuration as well as CO_2 and other greenhouse gases concentrations are set at pre-industrial values. Each simulation was started from the same equilibrated pre-industrial simulation[5] and was run for 500 years. NPP is integrated over the whole water-column and averaged over the last 100 model years.

At low eccentricity (EminPmax and EminPmin) the eastern Indian ocean surface dynamics is forced by the summer westerlies that blow northward over the Bay of Bengal (Extended Data Fig. 4f), associated with high precipitation over India and the Himalayan foreland region, while strong easterlies are recorded south of the equator. Winds force strong westward surface currents along the equator and south of Sumatra Island that generate upwelling (Extended Data Figure 7b). The latter advects nutrients to the surface (Extended Data Figure 7a) and triggers high productivity during summer. This peak productivity contributes to the strong seasonal cycle in this region. The winds reverse during boreal winter, triggering a second productivity bloom of lesser intensity (not shown). The productivity minimum is recorded during late spring when low-level winds along the equator are weak westerlies that favour downwelling and prevent strong convective mixing, which results in lower nutrient content within the surface layer of the ocean. The seasonal cycle of productivity in this region is very similar to the cycle simulated for the present-day equatorial Indian Ocean[5].

During high eccentricity periods at precession minima (maxima), increasing (decreasing) boreal summer insolation (Extended Data Fig. 5b-c) is responsible for increasing (decreasing) sea-level pressure over continental Asia (Extended Data Fig. 5d-h). Induced modifications of sea-level pressure gradients over the tropical Indian and Pacific Oceans in turn translate into changes in the low-level wind circulation over the Indo-Pacific Warm Pool, IPWP (Extended Data Fig. 4f-h). Anomalous easterlies at precession minima (westerlies at precession maxima) in the equatorial region generate anomalous upwelling along the equator (SW of India) that are responsible for the increasing nutrient content at the surface triggering large enhancement of productivity (Extended Data Figure 6a-c). NPP is, in addition, amplified by modifications of the hydrological cycle that create more favourable conditions related to changes in salinity, water temperature and/or amount of solar radiation at the surface. At maximum precession and eccentricity, for example, higher sub-surface salinity (+0.5 to 1.6 psu) and lower temperatures (-1.2 to -2°C) in the western Bay of Bengal (Extended Data Figure 7c) reduce stratification of the upper-water column, which favours vertical mixing and contributes to enhanced productivity. The simulated patterns of atmosphere-ocean circulation and surface ocean physical state (Extended Data Figure 4f-h and 6b-c) are in line with previous modelling study under similar orbital configurations[77-79]. In addition, our simulations also illustrate how these changes impact the seasonal productivity cycle. The increasing amplitude of the seasonal cycle in the surface ocean at high eccentricity is probably not limited to the IPWP area. For example, Erb et al.[80] also simulate enhancement of the surface ocean temperature cycle at high eccentricity in the Eastern Equatorial Pacific, with higher amplitude that in the Western Equatorial Pacific.

Methods references

39 Beaufort, L. Adaptation of the random settling method for quantitative studies of calcareous nannofossils. *Micropaleontology* **37**, 415-418 (1992).

40 Beaufort, L., Barbarin, N. & Gally, Y. Optical measurements to determine the thickness of calcite crystals and the mass of thin carbonate particles such as coccoliths. *Nature Protocols* **9**, 633-642, doi:10.1038/nprot.2014.028 (2014).

41 Beaufort, L. & Dollfus, D. Automatic recognition of coccolith by dynamical neural network. *Mar. Micropaleont.* **51/1-2**, 57-73 (2004).

42 Barbarin, N. *La reconnaissance automatisée des nannofossiles calcaires du Cénozoique,* PhD thesis, Aix-Marseille Université, (2014).

43 Beaufort, L. Weight estimates of coccoliths using the optical properties (birefringence) of calcite. *Micropaleontol.* **51**, 289-298 (2005).

44 Dollfus, D. *Reconaissance des Formes Naturelles par des Réseaux de Neurones Artificiels: Application au Nannoplancton Calcaire,* PhD thesis, Aix-Marseille Université, (1997).

45 Dollfus, D. & Beaufort, L. Fat neural network for recognition of position-normalised objects. *Neural Networks* **12**, 553-560 (1999).

46 Breiman, L. Random forests. *Machine learning* **45**, 5-32 (2001).

47 de Garidel-Thoron, T., Rosenthal, Y., Bassinot, F. C. & Beaufort, L. Stable sea surface temperatures in the western Pacific warm pool over the past 1.75 million years. *Nature* **433**, 294-298 (2005).

48 Shackleton, N. J. & al., e. An alternative astronomical calibration of the lower Pleistocene timescale based on ODP Site 677. *Transaction of the Royal Society of Edinburgh* **81**, 251-261 (1990).

49 Carcaillet, J. T., Thouveny, N. & Boulès, D. L. Geomagnetic moment instability between 0.6 and 1.3 Ma from cosmonuclide evidence. *Geophys. Res. L.* **30**, 1792 (2003).

50 Beaufort, L. & party, S. s. *MD148/PECTEN.* (Institut Polaire Francais, 2005).

51 Tachikawa, K. *et al.* The precession phase of hydrological variability in the Western Pacific Warm Pool during the past 400 ka. *Quaternary Science Reviews* **30**, 3716-3727, doi:10.1016/j.quascirev.2011.09.016 (2011).

52 Regoli, F. *et al.* Progressive shoaling of the equatorial Pacific thermocline over the last eight glacial periods. *Paleoceanography* (2015).

53 Clemens, S. C., Kuhnt, W., LeVay, L. J. & Scientists, t. E. Indian monsoon rainfall. *International Ocean Discovery Program Preliminary Report* **353**, doi:10.14379/iodp.pr.353.2015 (2015).

54 Clemens, S. C. Site U1443. - *Proceedings of the International Ocean Discovery Program; Indian monsoon rainfall; Expedition 353 of the riserless drilling platform from and to Singapore; Sites U1443-U1443, 29 November 2014-29 January 2015* **353**, 41-41 (2016).

55 Gebregiorgis, D. *et al.* Southern Hemisphere forcing of South Asian monsoon precipitation over the past ~1 million years. *Nature Communications* **9**, 4702, doi:10.1038/s41467-018-07076-2 (2018).

56 Gebregiorgis, D. *et al.* What Can We Learn From X-Ray Fluorescence Core Scanning Data? A Paleomonsoon Case Study. *Geochemistry, Geophysics, Geosystems* **21**, e2019GC008414, doi:10.1029/2019GC008414 (2020).

57 McGrath, S. M., Clemens, S. C., Huang, Y. & Yamamoto, M. Greenhouse Gas and Ice Volume Drive Pleistocene Indian Summer Monsoon Precipitation Isotope Variability. *Geophysical Research Letters* **48**, e2020GL092249 (2021).

58 Rosenthal, Y., Holbourn, A. E., Kulhanek, D. K. & Scientists, E. in *IODP proceeding* Vol. 363 (ed IODP) 69 (Texas A&M University, College Station TX, USA, 2017).

59 Beaufort, L., Bassinot, F. C. & Vincent, E. in *Reconstructing Ocean History : a window into the future* (eds F. Abrantes & A.C. Mix) 245-272 (Kluwer Academic/Plenum Publisher, 1999).

60 Young, J. R., P.R., B. & J.A., L. *Nannotax3 website*, <http://www.mikrotax.org/Nannotax3> (2021).

61 Perch-Nielsen, K. in *Plankton Stratigraphy: Volume 1, Planktic Foraminifera, Calcareous Nannofossils and Calpionellids* Vol. 1 (eds Hans M Bolli, John B Saunders, & Katharina Perch-Nielsen) (CUP Archive, 1989).

62 Beaufort, L., Probert, I. & Buchet, N. Effects of acidification and primary production on coccolith weight: Implications for carbonate transfer from the surface to the deep ocean. *Geochemistry, Geophysics, Geosystems* **8** (2007).

63 Lyle, M. Neogene carbonate burial in the Pacific Ocean. *Paleoceanography* **18**, doi:10.1029/2002PA000777 (2003).

64 Paillard, D., Labeyrie, L. & Yiou, P. Macintosh program performs time-series analysis. *Eos Trans. AGU,* **77**, 379 (1996).

65 Li, M., Hinnov, L. & Kump, L. Acycle: Time-series analysis software for paleoclimate research and education. *Computers & Geosciences* **127**, 12-22, doi:https://doi.org/10.1016/j.cageo.2019.02.011 (2019).

66 Blackman, R. B. & Tukey, J. W. The measurement of power spectra from the point of view of communications engineering—Part I. *Bell System Technical Journal* **37**, 185-282 (1958).

67 Thomson, D. J. Spectrum estimation and harmonic analysis. *Proceeding of the IEEE* **70**, 1055-1096 (1982).

68 Bollmann, J. Morphology and biogeography of the Gephyrocapsa coccoliths in Holocene sediments. *Mar. Micropaleontol.* **29**, 319-350 (1997).

69 Hourdin, F. *et al.* Impact of the LMDZ atmospheric grid configuration on the climate and sensitivity of the IPSL-CM5A coupled model. *Climate Dynamics* **40**, 2167-2192 (2013).

70 Krinner, G., Ciais, P., Viovy, N. & Friedlingstein, P. A simple parameterization of nitrogen limitation on primary productivity for global vegetation models. *Biogeosciences Discussions* **2**, 1243-1282 (2005).

71 Madec, G. & Nemo, T. NEMO ocean engine. *Note du Pôle de modélisation de l'Institut Pierre-Simon Laplace* **27** (2015).

72 Madec, G. NEMO reference manual, ocean dynamics component: NEMO-OPA. *Preliminary version. Note du Pole de modélisation, Institut Pierre-Simon Laplace (IPSL), France*, 1288-1161 (2008).

73 Fichefet, T. & Maqueda, M. M. Sensitivity of a global sea ice model to the treatment of ice thermodynamics and dynamics. *Journal of Geophysical Research: Oceans* **102**, 12609-12646 (1997).

74 Valcke, S. *et al.* Coupling technologies for earth system modelling. *Geosci. Model Dev* **5**, 1589-1596 (2012).

75 Dufresne, J.-L. *et al.* Climate change projections using the IPSL-CM5 Earth System Model: from CMIP3 to CMIP5. *Climate Dynamics* **40**, 2123-2165 (2013).

76 Mayorga, E. *et al.* Global nutrient export from WaterSheds 2 (NEWS 2): model development and implementation. *Environmental Modelling & Software* **25**, 837-853 (2010).

77 Bosmans, J. *et al.* Response of the Asian summer monsoons to idealized precession and obliquity forcing in a set of GCMs. *Quaternary Science Reviews* **188**, 121-135 (2018).

78 Braconnot, P. & Marti, O. Impact of precession on monsoon characteristics from coupled ocean atmosphere experiments: changes in Indian monsoon and Indian ocean climatology. *Marine Geology* **201**, 23-34 (2003).

79 Prescott, C., Haywood, A., Dolan, A., Hunter, S. & Tindall, J. Indian monsoon variability in response to orbital forcing during the late Pliocene. *Global and Planetary Change* **173**, 33-46 (2019).

80 Erb, M. P. *et al.* Response of the equatorial pacific seasonal cycle to orbital forcing. *Journal of Climate* **28**, 9258-9276 (2015).

81 Chen, M.-T. & Beaufort, L. Exploring quaternary variability of the east Asia monsoon, Kuroshio Current, and western Pacific warm pool systems: High-resolution investigations of paleoceanography from the IMAGES III (MD106) IPHIS cruise. *Terrestrial Atmospheric And Oceanic Sciences* **9**, 129-142 (1998).

82 Gartner, S. Paleoceanography of the mid-Pleistocene. *Mar. Micropaleontol.* **13**, 23-46 (1988).

83 Pujos, A. & Giraudeau, J. Distribution of Noelaerhabdaceae (calcareous nannofossils) in the upper and middle Quaternary of the Atlantic and Pacific oceans. *Oceanologica acta* **16**, 349-362 (1993).

Acknowledgments

This paper is a contribution of the Climate research group at CEREGE. This research uses samples provided by the International Ocean Discovery Program (IODP). We thank the scientists, technical staff, and crews of IODP Expeditions 353 and 363 and IMAGES Expeditions 3 and 13. The authors acknowledge French ANR projects CALHIS (LB), iMonsoon (CTB), AMOR (YD), and INSU project CALVE (CTB) which provided funding for this work. IODP-France provided post-cruise funding to LB and CTB. We thank A. Fruy and S. Sergi for sample preparation assistance. We thank the CEA/CCRT for providing access to the HPC resources of TGCC under the allocation 2019-A0070102212 made by GENCI.

Author Contributions

LB designed the study. LB, YG, NB and MT developed automated artificial intelligence methods. LB, CTB, JCM, PC, EG, and SB prepared samples and/or generated data. ACS designed and ran the model simulations, in collaboration with YD. LB and CTB analysed the morphometric data. LB, CTB, ACS, BSM, YD, and YR discussed interpretations. LB, CTB and ACS wrote the manuscript with important contributions from BSM, YD, and YR.

Competing interest declaration

The authors declare no competing interests.

Extended Data Figures and Tables

Extended Data Table 1: Characteristics of the nine marine records used in this study. Biome codes[25]: INDE = Eastern India Coastal province, MONS = Indian Monsoon Gyres Province, WARM = Western Pacific Warm Pool province, SUND = Sunda-Arafura Shelves Province, AUSE = East Australian Coastal Province, ISSG = Indian South Subtropical Gyre Province. These cores were retrieved during four expeditions: IMAGES 3[81] and 13[50], and International Ocean Discovery Program (IODP) Expeditions 353[53] and 363[58], which took place in the Western Pacific and Indian tropical oceans (Figure 3a).

Extended Data Table 2: Relative calcium carbonate mass contribution per calcareous nannofossil taxon/groups for each sediment core. In each case, values represent the average value of the entire time series. Values were calculated by multiplying the number of individuals recognized for each taxon (class[42] grouped by taxon : Noelaerhabdaceae (*Emiliania, Gephyrocapsa, Pseudoemiliania* and *Reticulofenestra*), Coccolithales (*Calcidiscus, Coccolithus,and Umbellicosphaera*), and Helicosphaerales + Syracosphaerales

(*Helicosphaera, Pontosphaera, Syracosphaera* and *Rhabdolithus*)) multiplied by the averaged mass of the considered class in that core. This calculation was not possible for core MD05-2930 as some species abundance data were not available.

Extended Data Table 3: Summary of orbital parameters[23] used for each simulation and Mean Yearly Contrast of Radiation at Equator (Wm^{-2}) derived from IPSL-CM5A2 (Methods).

Extended Data Figure 1: Size and MDI records for each core. Top panels **a** to **i**: Size frequency plots for each individual core used to create the composite record shown in Figure 1a. Lower panels **a** to **i**: Individual MDI records for each core (black lines and points) plotted with the stacked MDI record (red line). Pearson correlation coefficients between individual sites and the stack vary between 0.71 and 0.93 (p-values are all <0.00001).

Extended Data Figure 2: **Time-series analyses of individual records**. **a**: Cross-spectral analysis between eccentricity and stacked coccolith length. Top: coherency; Bottom: phase (radian). **b to j**: MTM and evolutive spectral analyses (see Methods) of detrended individual MDI series resampled at 2 kyr intervals (shown on left of each evolutive analysis). Primary orbital periods are shown by red lines.

Extended Data Figure 3: **Decomposition of the Noelaerhabdaceae mass accumulation rate (NoMAR) record into its mass and flux components**. **a**: Stacked NoMAR record, binned into 2-ky intervals (orange shading) and smoothed with a 30-kyr moving window (orange line), **b**: Noelaerhabdaceae coccolith flux (blue) and average Noelaerhabdaceae coccolith mass (red). Here, stacked mass and flux records are smoothed with a 30-kyr moving window as in **a**. **c**: NoMAR (orange) and MDI (purple) records, smoothed with a 30-kyr moving window. Grey shaded areas represent four described acmes of mid-size Noelaerhabdaceae species[19-21,82,83].

Extended Data Figure 4: **Ocean-atmosphere model outputs under different orbital configurations:** Top: Yearly maximum contrast in NPP (gC m^{-2} day^{-1}) for **a**: EminPmin, **b**: EmaxPmin and **c**: EmaxPmax. Low eccentricity values minimize the amplitude of precession variability, thus we only show results for minimum precession value at minimum eccentricity (EminPmin) but the reader can consider those results to be similar for the EminPmax simulation. **d** and **e** represent the anomaly of yearly maximum contrast in NPP. At EmaxPmax, the eastern equatorial Indian Ocean exhibits moderate seasonality (**a**) due to inhibition of the summer productivity induced by lower nutrient concentrations in this area (Extended Data Fig. 6a). In this case, high productivity areas during boreal summer are shifted to south-west of India. Bottom: Late summer (JASO) low-level winds for **f**: EminPmin, **g**: EmaxPmin, **h**: EmaxPmax simulations. **i** and **j** represent the anomaly in late summer low-level winds. At EmaxPmax the north-equatorial westerlies (**c**, **e**) are confined to south of 10°N due to the extension above India of the low-pressure area.

Extended Data Figure 5: **Solar radiation and sea-level pressure in model simulations.** Seasonal latitudinal variations of solar radiation at the top of the atmosphere derived from the model ($W.m^{-2}$); **a**: EminPmin, **b**: EmaxPmin, **c**: EmaxPmax. See Extended Data Table 3 for details of orbital configurations of each simulation. Late summer (JASO) low-level winds for **d**: EminPmin, **e**: EmaxPmin, **f**: EmaxPmax simulations and anomaly in late summer low-level winds, **g**: EmaxPmin minus EminPmin, **h**: EmaxPmax minus EminPmax.

Extended Data Figure 6: **Nutrients, temperature, and upwelling in model simulations. a**: NO_3 concentrations in the surface layer (0-100m), **b**: upwelling velocity (averaged between 40 and 80m), **c**: Sea Surface Temperature (SST). All variables are averaged over JASO. **Left**: Emin, **Middle**: EmaxPmin minus EminPmin, **Right**: EmaxPmax minus EminPmax.

Extended Data Figure 7: **Explanation of non-linearities in coccolithophore evolution a**: Low-pass filter design, for the delay between First Appearance Datum (FAD) and the beginning of the acme (BA) for *E. huxleyi* (blue line, lag of two eccentricity cycles) and another possible scenario for another species (red line, lag of one eccentricity cycle). The stepped green line represents *E. huxleyi*'s existence (0 means absence, 1 means presence). The blue and red curves in all panels are the output series of the 2 low-pass filters described in the methods. The black curve in **a** represents coeval eccentricity values. **b** and **c**: Bode plots of the 1-cycle lag filter (red) and the 2-cycle lag filter (blue) for magnitude (**b**) and phase (**c**) (see Methods). Earth's primary orbital periods are indicated by shading.

Data and Code availability

All coccolith morphological data, as well as all model outputs described in the paper (including NPP and main oceanic and atmopsheric variables) are archived at www.pangaea.de.

LMDZ, XIOS, NEMO and ORCHIDEE are released under the terms of the CeCILL license. OASIS-MCT is released under the terms of the Lesser GNU General Public License (LGPL). IPSL-CM5A2 source code is publicly available through svn, with the following commands line :svn co http://forge.ipsl.jussieu.fr/igcmg/svn/modipsl/branches/publications/IPSLCM5A2.1_11192019 modipsl ; cd modipsl/util ; ./model IPSLCM5A2.1

The mod.def file provides information regarding the different revisions used, namely :

- NEMOGCM branch nemo_v3_6_STABLE revision 6665
- XIOS2 branchs/xios-2.5 revision 1763
- IOIPSL/src svn tags/v2_2_2
- LMDZ5 branches/IPSLCM5A2.1 rev 3591
- branches/publications/ORCHIDEE_IPSLCM5A2.1.r5307 rev 6336
- OASIS3-MCT 2.0_branch (rev 4775 IPSL server)

The login/password combination requested at first use to download the ORCHIDEE component is anonymous/anonymous. We recommend that you refer to the project website: http://forge.ipsl.jussieu.fr/igcmg_doc/wiki/Doc/Config/IPSLCM5A2 for a proper installation and compilation of the environment.