Diversity decoupled from ecosystem function and resilience during mass extinction recovery

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The Chixulub bolide impact 66 million years ago drove near-instantaneous oceanic ecosystem collapse. Devastating diversity loss at the base of ocean food-webs likely triggered cascading extinctions across all trophic levels[1–3] and caused severe disruption of ocean biogeochemical function, especially the cycling of carbon between the surface and deep sea[4,5]. The absence of sufficiently detailed biotic data spanning the post-extinction interval has limited our understanding of how ecosystem resilience and biochemical function was restored, with estimates of 'recovery' varying from <100 years to 10 million years[6–8]. Using a 13-million-year long nannoplankton time-series we show that post-extinction communities exhibited 1.8 million years of exceptional volatility before a more stable equilibrium community emerged displaying hallmarks of resilience. The transition to this new equilibrium-state community with a broader cell-size spectrum coincides with indicators of carbon cycle restoration and a fully functioning biological pump[9]. This finding implies a fundamental link between ecosystem recovery and biogeochemical cycling over timescales that are longer than those suggested by proxies of export production[7,8] but far shorter than the return of taxic richness[6]. That species richness remained low as both community stability and biological pump efficiency re-emerged, suggests that ecological function rather than number of species is more critical to community resilience and biochemical function.

The end Cretaceous bolide impact stripped the ocean of diversity and biogeochemical function[1] more abruptly than any other mass extinction event, including the current anthropogenically-induced crisis. Following >90% species extinction in calcifying plankton[3], the immediate aftermath of the impact saw oceans repopulated by aberrant communities dominated by ephemeral species, atypical in ecology, physiology and cell size[9–11]. Over time a diverse, biochemically-functioning and resilient ecosystem was re-established. This wholesale re-assembly of the ocean ecosystem provides clues to the essential attributes that

44 underpin stable ecosystems and maintain robust ecological states and function[12,13]. However,
45 assessments of when this ecosystem 'recovery' was achieved vary widely in definition and
46 duration. Export production proxies imply virtually instantaneous restoration of at least some
47 biogeochemical functionality (<100 years)[7,8], while the return of species richness to pre-
48 extinction levels suggests recovery 8-10 million years (Myr) later[6]. Here, we track the post-
49 extinction path to ecosystem restoration by building an exceptional, high-resolution 13-
50 million-year community record of calcareous nannoplankton, the dominant fossil-forming
51 primary producers. Much of the marine food-web leaves little or no fossil remains, but the
52 biomineralised exoskeletons of calcareous nannoplankton provide a remarkable proxy for
53 basal ecosystem health during past environmental change events (see ref. 3 and refs therein).
54 Our new nannoplankton record bridges the temporal range of current recovery estimates and
55 allows us to target measures of community *stability* (the level of deviation around the average
56 state, see Methods) and *resilience* (the ability to resist and recover from perturbation[14]) as
57 they re-emerged. The record from Ocean Drilling Program (ODP) Site 1209 in the Pacific
58 Ocean (Extended Data Fig. 1, Methods) has highly-resolved orbital age control (see Methods)
59 and complementary proxy data for environmental change and biogeochemical function. Our
60 plankton data comprise a sample every ~13 thousand years, spanning 13 Myr, with around
61 700,000 fossil counts providing an unprecedented time-series of key community parameters,
62 including abundance, diversity, taxic richness, variance, dissimilarity and body size (see
63 Methods).

64 Our data and analyses reveal striking temporal trends in nannoplankton community structure
65 and resilience (Fig. 1). Most visually obvious is the differentiation of a highly volatile post-
66 extinction interval of ~1.8 Myr, from a subsequent more 'stable' background state (Fig. 1e),
67 conspicuous in the Summed Coefficient of Variation metric (Σ_{CV}). We primarily focus on this
68 metric which quantifies the level of variance or 'stability' in relative abundances (see
69 Methods) but as community stability is a multi-faceted concept, we also refer to other indices
70 including community dissimilarity (Bray-Curtis Dissimilarity) and diversity (Simpson's
71 index of dominance/evenness). These measures of community structure all point to the state-
72 shift ~1.8 Myr post-impact (Fig. 1, Extended Data Fig. 2) and an early Danian interval
73 characterized by exceptional fluctuations that are statistically distinct from the rest of the
74 record (Extended Data Fig. 2), hereafter referred to as Regime 1 (66.0-64.2 Myr ago) and
75 Regime 2 (64.1-53.0 Myr ago). When we compare Σ_{CV} with carbon isotope ($\delta^{13}C$) excursion
76 magnitude, a proxy for environmental change (Fig. 2, see Methods), the two regimes show
77 strikingly different relationships with environmental forcing. The earliest Danian (Regime 1)
78 exhibits no relationship between Σ_{CV} and $\delta^{13}C$ magnitude, with prolonged high-amplitude
79 variance largely the statistical impact of a series of ocean-wide abundance acmes[10,15,16] (Fig.
80 3a, b, Extended Data Figs 3, 4), occurring alongside very little apparent environmental
81 perturbation (Fig. 1a, 2). This interval saw very short-term (<<100 kyr) impact-related
82 environmental changes[17,18] (cooling over <50 years, ref 17, and warming through <100 kyr,
83 ref 18), waning Deccan trap volcanism over 600 kyr (e.g., ref. 19), and only two notable
84 environmental change events – the lower-C29n and Dan-C2 hyperthermals - all occurring or
85 ceasing well before the interval of high variance comes to an end. Therefore, the disconnect
86 between community metrics and indicators of climate variability suggests that environmental
87 changes were not driving and maintaining the high levels of biotic variability through this
88 1.8-million-year interval. In contrast, above this level (Regime 2), $\delta^{13}C$ magnitude is a strong
89 predictor of community variance ($R^2 = 54\%$ on first differences, Fig. 2) with the majority of
90 data forming a 'background' grouping punctuated by variance peaks associated with
91 hyperthermal events[20] (highlighted in red in Figs 1a, c, Fig. 2). This indicates that by the late
92 Danian, nannoplankton communities were fluctuating around some steady state and

93 demonstrate indicators of resilience[14], including proportionate responses to environmental
94 perturbation (i.e., the significant linear trend between carbon isotope excursion and variance)
95 and rapid recoveries following each event (return of variance to the background state within
96 <200 kyrs of the excursion, Fig. 1c and ref 21).

97 Tantalisingly, the shift to more stable communities approximately 64.2 Myr ago (the end of
98 Regime 1) also falls towards the top of the interval of biological pump recovery[9] (Fig. 3f).
99 Ocean biogeochemical function was profoundly disrupted by the end-Cretaceous mass
100 extinction, most obviously through weakening of the biological pump[2,5,9]. The scale and
101 duration of this productivity reduction is contentious, ranging from scenarios of a lifeless
102 *Strangelove Ocean* to a partially functioning *Living Ocean* state[4], but the long, multimillion-
103 year delay in restoration of the biological pump is well established[2,22], and indicated by both
104 the gradual increase in vertical carbon isotope gradient to pre-extinction values[9] and changing
105 community structures of benthic primary-consumer communities (benthic foraminifera)[23].
106 Carbon isotope gradients finally returned to pre-extinction values by ~1.77 Myrs after the
107 event[9] providing an upper limit on full recovery of the biological pump. This broad
108 concurrence between biological pump restoration and the shift to a more stable plankton
109 community background state (Fig. 3) provides strong evidence for an intrinsic link between
110 biological recovery of the ecosystem and its calibre of biochemical functioning. We can
111 augment this understanding of ecosystem recovery and efficient biological pumping by
112 exploring the roles of the post-extinction taxonomic rebuild and rapid cell-size increases
113 using new, high-resolution species richness data (Fig. 3d; see Methods) and reconstructions
114 of nannoplankton community cell volume (Fig. 3e; see Methods).

115 Mean community cell volume and species richness exhibit pulsed patterns through the
116 Danian, both showing rapid increases in the first half million years after the mass extinction,
117 from initially extremely low species numbers and predominantly very small cells (Fig. 3d, e).
118 Rapid diversification within Regime 1 saw the appearance of >15 species alongside a peak in
119 cell volume around 300 kyr after the extinction level dominated by cells of heavily calcified
120 calcareous dinoflagellates. A second phase of cell-volume increase occurred as carbon export
121 gradually returned to pre-extinction values, and was driven by both diversity and ecology,
122 with relative abundance increases in existing large taxa (such as *Coccolithus,* Extended Data
123 Fig. 3) and the addition of larger new species across all of the emerging clades (Fig 3d).
124 Modern observations indicate that phytoplankton community size structure is a critical
125 control on export flux and, further, that nannoplankton mineral ballasting significantly
126 increases the transfer efficiency of carbon[24-26]. The shift to larger cells and ballast biominerals
127 seen in our early Danian cell size record (Fig. 3e) would therefore have contributed to
128 increased carbon export flux with stable, diverse communities delivering this flux more
129 consistently through space and time, and supporting greater size diversity in the
130 zooplankton[26]. The role of larger zooplankton and the production of fast-sinking faecal
131 pellets in these evolving export pathways is more difficult to reconstruct due to poor fossil
132 records. However, an indication of higher trophic level disruption is seen in the early Danian
133 zooplanktonic foraminifera where low diversities, acme fluctuations and small body size are
134 observed across similar timescales to the recovery of the biological pump[11,27]. Finally, a third
135 phase of cell volume increase coincides with a major expansion of ecological diversity
136 marked by the appearance of the first specialist oligotrophic nannoplankton since the mass
137 extinction (Discoasterales; ~3.5 Myr post-extinction; Figs 1b, 3a, d, e, Extended Data Fig. 4;
138 ref 28) and re-introduction of photosymbiotic strategies in planktonic foraminifera (~2.5 Myr
139 post-extinction; Fig. 3f; ref 9). Diversification then continued, with species richness only
140 reaching pre-extinction levels at 10 Myr after the mass extinction (~56 Myr ago; Fig. 1g).

The scale of ecosystem collapse at the K/Pg event and protracted recovery of resilience, diversity and biogeochemical function, demonstrates the singular consequences of mass-extinction-level change and subsequent durability of ecosystems following restoration. Predictions of contemporary mass-extinction[29] detail accelerating declines in ecosystem functioning as diversity falls[30,31]. We show here that this relationship also holds in reverse as biodiversity reboots after a mass extinction. Early but modest taxic and trait (especially size) diversification within the recovering biota re-established ecosystem stability with links to functioning (specifically the biological pump) long before species richness and ecological diversity returned to pre-extinction levels. Rapid biotic turnover and community instability during this reboot increased the probability of biotically-forced evolution alighting on organisms capable of fulfilling essential functional roles, which in turn facilitated community recovery and the re-emergence of ecosystem stability. Ecosystem stability is therefore not determined by sheer numbers of species, but rather through the establishment and/or retention of key functional taxa fulfilling vital ecological and/or biogeochemical roles.

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Figures:

240 **Figure 1. Nannoplankton abundance, variability and diversity records from the latest**
241 **Cretaceous to early Eocene. a**, Carbon stable isotopes, dark green – benthic[32], lighter green
242 - bulk (see references in 21). **b**, Summary of main nannoplankton clade abundances
243 determined for 981 samples. **c**, Summed coefficients of variation (Σ_{CV}) using 150 kyr moving
244 window (see Methods), separated into the early Danian (Regime 1, blue) and the rest of the
245 record (Regime 2, grey and red). The Cretaceous to K/Pg data points are in black. Triangles
246 (colour-coded by regime, black for the K/Pg window) show values for the named climate
247 events, which for the Eocene hyperthermals were calculated across the event duration (<150
248 kyr). Event nomenclature follows references given in the Methods. The vertical black dashed
249 line indicates estimated background level (<2.5 Σ_{CV}) based on the ranked order inflection
250 point on (**d**) with above-'background' data highlighted in red in **c**. **e**, Ranked-order plot of
251 Regime 1 datapoints where the dark red dashed line indicates an inflection point at the higher
252 end of the Σ_{CV} values (marked on **c**). **f**, Calcareous nannoplankton species richness at 250 kyr
253 resolution (see Methods).

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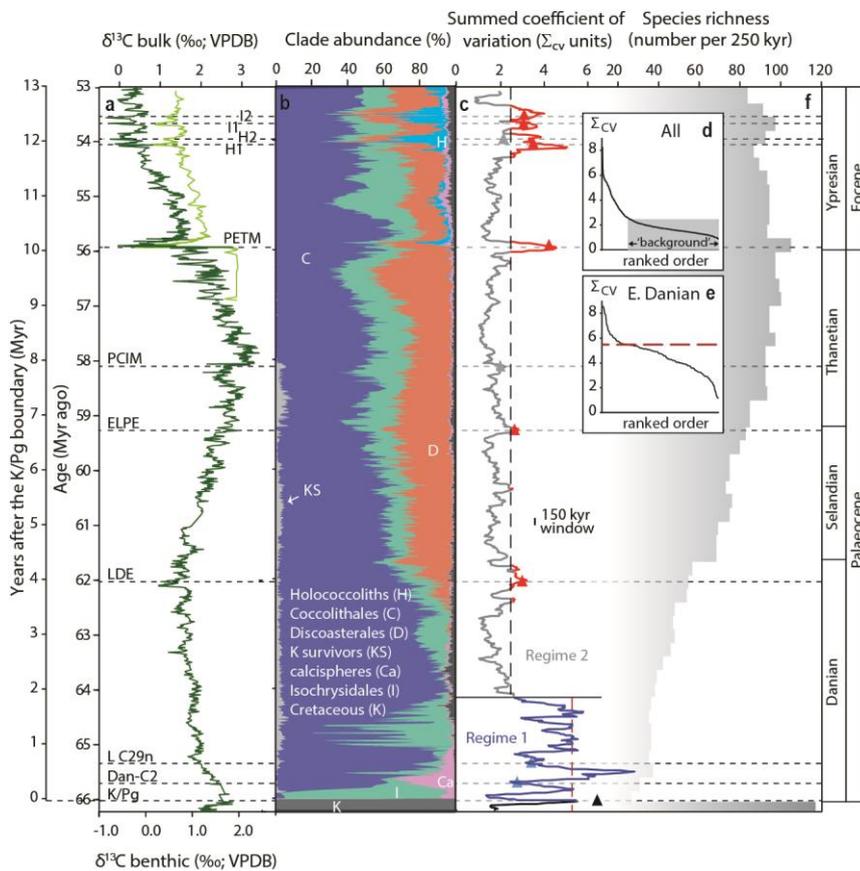
Figure 2. Σ_{CV} and magnitude of climate perturbation ($\delta^{13}C$ excursion). a, raw data. **b,** first differences. The Σ_{CV} values are plotted for each named climate event (using the highlighted values in Fig. 1c, here shown as triangles in a) and every intervening ~150 kyr. Data-points are separated into Cretaceous (black, n = 2, not included in **b**), early Danian (blue, 66 to 64.2 Myr ago, Regime 1, n = 23) and the rest of the record (grey and above background in red, Regime 2, n = 71, from Fig. 1c, d). Regime 1 Σ_{CV} shows no relationship with climatic perturbation (blue trend-line in **b**), unlike Regime 2 (generalised least squares trend-line for all grey plus red data-points, n = 71, grey dashed line in **a** and **b**), which is significant in both the raw data (**a**) and on first differences (**b**) (R^2 = 31% and 52%, respectively (see Methods). The inferred background level of 2.5, based on rank ordering (Fig. 1d), is indicated by the grey box.
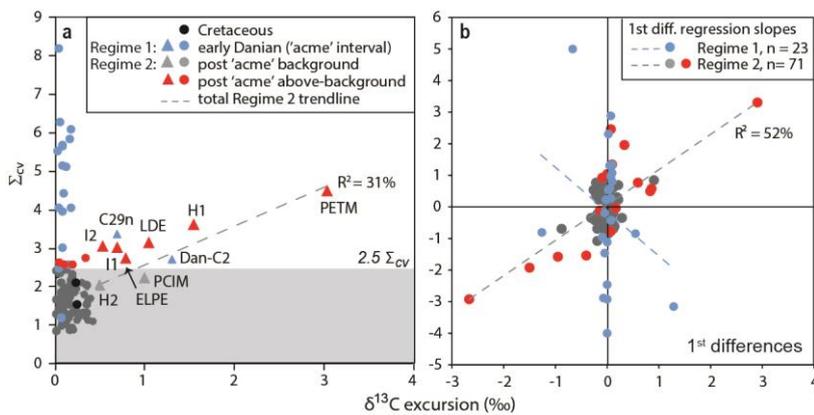
Figure 3. Danian nannoplankton community variance, acme abundances, diversity, cell volume and key milestones. a, Abundance records of the early Danian coccolithophore acmes and Discoasterales (*Sphenolithus* and *Fasciculithus*), **b**, Σ_{CV} (Regime 1 in blue, Regime 2 in grey and red) and Danian climate events. **c**, Community diversity (Simpson's index), 150 kyr moving average in grey. **d**, Global species richness resolved at 100 kyr scale (see Methods). **e**, Estimated average (mean) cell volume and estimated particulate inorganic carbon content (PIC) of the calcareous nannoplankton (grey), excluding calcispheres (black) (see Methods). Cell size maxima at 300 kyr and 4.25 Myr after the K/Pg given in grey italics. Key milestones/observations from herein and from published records are indicated (see Methods). *The level for the end acmes is taken as the top of the *Praeprinsius* acme. **f**, Carbon isotope gradient ($\Delta\delta^{13}C$) between Walvis Ridge (WR, ODP Site 1262) planktonic and benthic foraminifera species (ref 9, using adjustment option 2), grouped according to ecology (blue – surface survivors, green – surface symbiotic, orange – thermocline, black – mixed layer, grey – transitional).
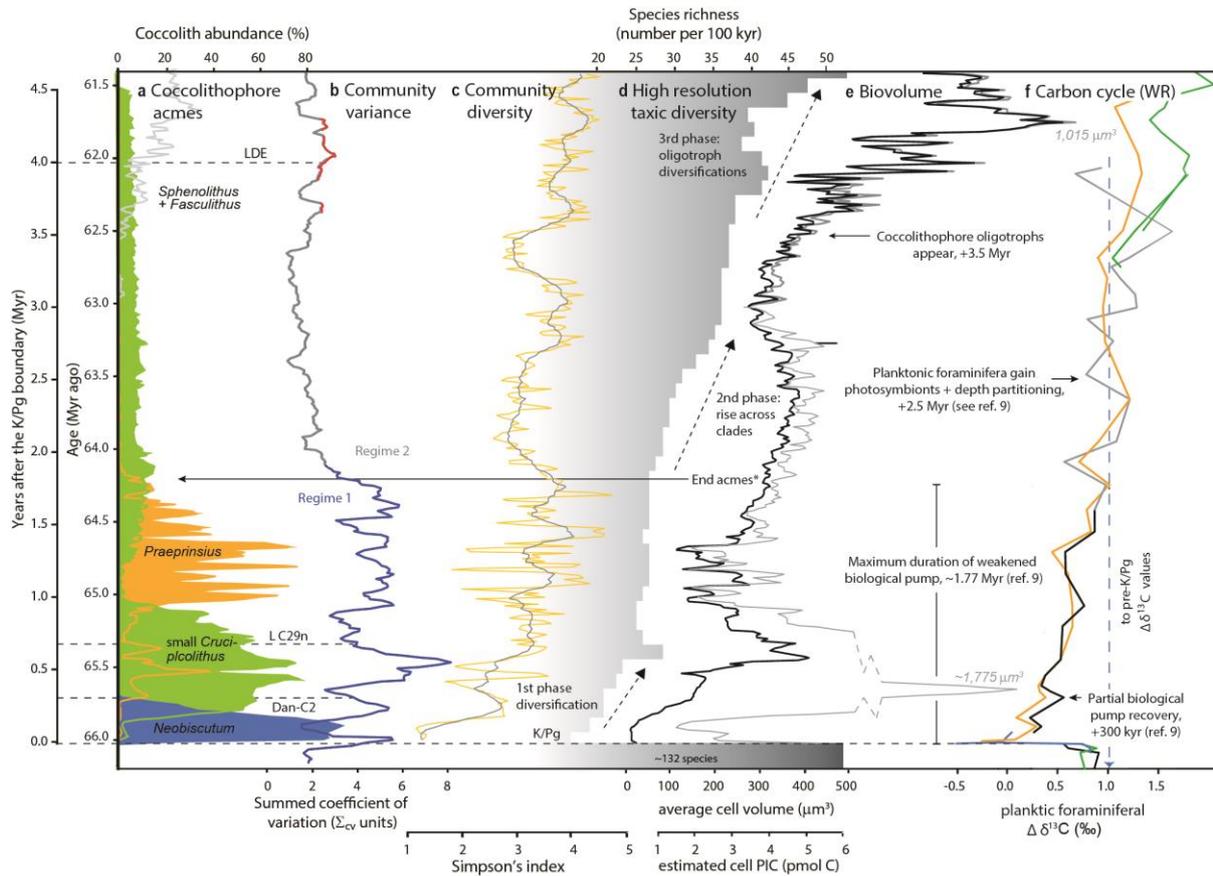
METHODS

Experimental Design. Our objective was to characterize the emergence of resilience in plankton communities in the aftermath of the Cretaceous-Palaeogene (K/Pg) mass extinction and assess implications for higher trophic levels and biogeochemical cycling of the oceans. This work is the first palaeoecological study to present sustained very-high resolution sampling (13 kyr) over such a long duration (13 million years), maintaining sampling intensity across both event and background stratigraphic intervals. To achieve this, we required a continuous long time-series record from a single location that was representative of global patterns, all features satisfied by the open ocean, gyre location of Ocean Drilling Program (ODP) Site 1209. The palaeogeography and overall oceanic setting varied little at this site across the 13 Myr record and calcareous nannoplankton provide the most consistent, high abundance fossil record of nannoplankton. This site has an orbitally-resolved age model, providing millennial sampling precision alongside high-resolution geochemical proxy records of palaeoenvironmental change[31]. Furthermore, the site is far from the Yucatan bolide impact and samples the dominant ocean basin of the early Cenozoic, providing the potential to track marine ecosystem recovery on a quasi-globally representative basis (see *c*GENIE section below).

Sampling strategy. The nannoplankton assemblage data come from a ~54 metre section of the composite splice[33] at ODP Site 1209 Shatsky Rise, in the palaeo-subequatorial Pacific Ocean (Extended Data Fig. 1). 981 samples were taken at ~13 kyr intervals, extending from the K/Pg boundary (66 Myr ago) through to the Palaeocene-Eocene Thermal Maximum (PETM: 56 Myr ago) and overlap the Eocene record of ref 21, giving a 13-Myr long record in total. Ages assigned to each sample use age models constructed for ODP Site 1209 by ref 34 and ref 35 (option 2), updated by ref 32. The age model uses tie-points in the $\delta^{13}C$ data correlated with the orbitally-tuned stratigraphy of ODP Site 1262, as summarized by ref 20 and ref 32.

Assemblage data. Smear slides were prepared for nannofossil observation using standard techniques[36]. Assemblage data (Extended Data Fig. 3) are based on statistically significant counts of 500 to 1000 nannofossil liths per sample across a minimum of 10 fields of view, following identical count and taxonomic protocols of the Eocene record from ref 21 (~218.5 to 208.0 rmcd, ~56 to 53 Ma). The assemblage data were counted to generic level, with some additional division into useful morphogroups (e.g., determined by genus and size, see below). Taxonomy generally follows refs 37–39. Visual assessment of preservation, as well as quantitative counts of lith fragmentation and presence of delicate lith structures, indicates that the nannofossils are generally well preserved but show some signs of etching and minor overgrowth, as is typical for carbonate-rich deep-sea sediments. Etching of delicate central area structures, particularly of Prinsiaceae specimens is common, but does not inhibit identification to genus level. While there is always some degree of variation in preservation quality through a long time-series such as this, our observations show that dissolution has not disproportionately distorted the assemblage character at any particular level or interval. This includes the hyperthermals where carbonate dissolution often increases (see ref 21) and, conversely, the immediate post-K/Pg interval where indicators suggest enhanced preservation[40]. Of note, the later absence of the exclusively-small taxa, *Neobiscutum,* small *Praeprinsius* and *Futyania*, is an evolutionary signal confirmed in sections worldwide[15], rather than a preservational artefact. There is evidence of reworking of Cretaceous taxa

333 immediately above the K/Pg boundary at Site 1209 (Extended Data Fig. 3), but these
334 specimens have not been included in the relative abundance calculations.

335 **Summed coefficient of variation (Σ_{CV}).** We have used a range of approaches (see below) to
336 characterise community structure but focus on the Σ_{CV} time-series as it best encapsulates the
337 key trends in community variance and relationships with environmental perturbation. The
338 Σ_{CV} method is an analytical technique that is independent of taxic composition, and enables
339 efficient collection and integration of large amounts of abundance data giving equal
340 weighting to each of the taxa included[21]. When applied to microfossil data, it highlights the
341 nuances of biotic response across a very broad spectrum of perturbations. We follow the
342 same procedure as ref 21 but without using the SiZer smoothing step because we are not
343 comparing datasets from different sources. First, the assemblage data, collected from samples
344 taken every ~5.5 cm (equivalent to every 13 kyr) were placed on the age scale and linearly
345 resampled using *AnalySeries version 2.0*[41] to provide consistent 13 kyr spacing between
346 datapoints. Second, we determined which taxa would be included for subsequent Σ_{CV}
347 analysis. Because the 13 Myr record includes significant evolution in community taxon-
348 makeup, we divided the section into million-year bins and determined the most abundant and
349 consistently present (>65% of samples) taxa in each. This resulted in the selection of 8 taxa
350 across each bin - a relatively low number because of the low diversity in the early Danian but
351 representing >95% of the total population in each sample. We then followed the Σ_{CV} method
352 of calculating coefficients of variation summed across these taxa using a moving window
353 duration of 150 kyrs. As the Σ_{CV} metric quantifies the levels of variance across multiple taxa,
354 our use of the term stability here refers to consistent and low levels of change in the
355 abundance distribution across the main taxa. The term stability is used in ecology in a myriad
356 of ways but in this case, we use a simple and intuitive definition of stability as meaning a
357 system with low variability (i.e., little deviation from its average state; following ref 42) - a
358 definition we think is most directly applicable to geological time-series data.

359 **Σ_{CV} sensitivity tests.** We have applied a range of sensitivity tests to the Σ_{CV} metric record,
360 examining for the effects of sample window duration, taxon dominance, ancestry, fossil
361 preservation, sedimentation rate and hiatuses (see also ref 21). Extended Data Figure 5
362 explores the impact of varying window duration and reveals how variance is packaged
363 through time, as well as any differences resulting from analysing the data in time *versus* age
364 domains. Σ_{CV} *increases* with increasing window-duration in the lower Danian, indicating that
365 the window is capturing additional variance that is spread throughout the interval. By
366 contrast, Σ_{CV} *decreases* with increasing window-duration across the PETM and ETM2,
367 indicating focused variance, with little additional variance in the broader time window
368 diluting the signal. We have explored the impact of shared ancestry because our analyses give
369 equal weight to each taxonomic unit potentially introducing artificially high variance. We
370 have tested for this by re-analysing the data using two additional models of shared ancestry
371 developed from our genus-level stratophenetic tree (Extended Data Fig. 6). Sensitivity of the
372 Σ_{CV} metric decreases as more genera are grouped, damping levels of variance (Extended Data
373 Fig. 7), particularly when merging abundant genera from the same family (the highly
374 conservative ancestry Option 1). However, the main patterns of variance still remain as
375 robust features (as they do in the dissimilarity index described below), particularly when
376 more branches of the tree are conserved (the moderately conservative ancestry Option 2).

Dissimilarity and diversity metrics. We have calculated additional metrics of assemblage structure, namely Bray-Curtis Dissimilarity (BC; a metric that highlights structural differences in abundance and composition); the Simpson's index (SI; an evenness/dominance metric that incorporates abundance distribution and taxic richness), and the standard deviation (variance) of the SI (Extended Data Fig. 2). BC was performed on the maximum and minimum abundance values across the 11 samples within each moving 150 kyr window, returning the maximum dissimilarity value. The values have been plotted for each moving 150 kyr window through the time-series. BC is sensitive to taxonomic turnover (shown by increasing values with increasing window size, Extended Data Fig. 5b) but the impact is minimised using the 150 kyr window, as species turnover is low. The standard deviation (variance) of SI was calculated from the 11 samples in each 150 kyr moving window. The Σ_{CV} and BC time-series patterns are very similar (R^2 of 63%) but the BC record differs in the amplitude of variation through background intervals because it is influenced, to varying degrees through the time-series, by rare taxa. SI is also highly sensitive to rarer taxon abundances and the rare, variable occurrences of taxa close to their appearance and/or disappearance.

Species richness estimates. The new species richness diversity data is an update of the global compilation of ref 3. We have added new taxa described since 2004, increased the temporal resolution to 250 kyr stratigraphic bins for the entire dataset (Fig. 1 and Extended Data Fig. 4) and 100-kyr bins for the Danian (Fig. 3), and present the data on the GTS2012 timescale[43]. The species richness is the total number of taxa that occur for some part of, or throughout, each stratigraphic bin. Species richness estimates are dependent on the bin duration, hence the difference between the values in Figures 1f and 3d.

Cell size and volume. Estimates of average cell volume (Fig. 3 and Extended Data Fig. 4) are based on mean cell size per taxon weighted according to their abundance in the community at any given time.

Average cell volume = $((((\%T1_{ra} \times \Theta T1_{av}) + (\%T2_{ra} \times \Theta T2_{av}) + (\%T3_{ra} \times \Theta T3_{av}) \ldots .. Tn]/2)^3)/3 \times 4\pi)/\Sigma\%T_{ra}$

Where % $T1_{ra}$ is the % relative *cellular* abundance of the taxon in the total assemblage and $\Theta T1_{av}$ is the average cell diameter of the taxon.

Cell diameter uses the internal diameter of coccospheres and cellular abundances were estimated by dividing the relative abundance of liths present by the average number of liths per cell. Coccosphere size and lith number for each taxon use (i) direct coccosphere measurements from coeval samples at ODP Site 1209 (Shatsky Rise), and also from Integrated Ocean Drilling Program (IODP) Sites 1403 and 1407 (North Atlantic), and from published scanning electron microscope (SEM) images of coccospheres[44,45]; (ii) coccolith measurements from these same samples converted to estimated cell size (and associated lith number) based on taxon-specific relationships between lith size, lith number and cell size determined from Palaeogene taxa within the same genus or family[46]; or (iii) estimates using modern analogues[46] (details in Extended Data Table 1). For the calcareous dinocysts, we took a conservative estimate of cell diameter of 20 microns, based on light microscope and SEM images of complete dinocyst coverings from the lowermost Danian of ODP Site 1210 (Shatsky Rise) and divided raw calcareous dinocyst fragment counts by 12, as an estimate of how many fragments constitute a whole cell. Estimated particulate inorganic carbon per cell uses the least-squares linear regression between cell volume and cell PIC in Figure 4c of ref. 46.

_c_GENIE Earth system modelling and palaeo-hydrographic location of Site 1209. We illustrate the palaeo-hydrographic location of Site 1209 using the '_c_GENIE' Earth system model. In this simulation, _c_GENIE is configured with late Maastrictian boundary conditions of continental configuration, bathymetry, and wind stress as described in ref 47. Additionally, the solar constant is reduced appropriate for 66 Myr ago and atmospheric CO_2 is set to 1112 ppm (×4 pre-industrial). We take the 10 kyr spin-up described in ref 47 and run this on for 10 more years, showing the results of the last year of the 10-year follow-on experiment in Extended Data Figure 1 as an annual average. ODP Site 1209 was slightly to the north (ca. 8°) of the palaeo-Equator 66 Myr ago (Extended Data Fig. 1a), lying towards the edge of an ocean current field that is circumequatorial (Extended Data Fig. 1b) and links the major ocean basins. In the simulated late Maastrictian climate, temperatures do not fall more than about 6°C cooler than those at the location of Site 1209 (35°C), nor exceed this, anywhere along the flow path by more than a few degrees C. Further, from simple visual inspection of the _c_GENIE simulations (Extended Data Fig. 1), the deflection of the circumequatorial current south of China and SE Asia to latitudes of ca. 10°S and interaction with the South Pacific subtropical gyre, suggest the potential for significant surface-water mixing to occur between the hemispheres. We conclude from this that Site 1209 is likely to be sampling the same tropical and partly sub-tropical plankton communities that occur in all major ocean basins and both hemispheres. The area of connected waters in the 28-38°C range is over 50% of the global ocean surface. The obvious exceptions to this global connectivity are the Arctic (being characterized by much cooler temperatures) and the South Atlantic (which exchanges with the Pacific primarily only to the South of Africa, with the cooler water regime in this ocean gateway representing a potential barrier to the mixing of tropical plankton communities globally).

Palaeogene climate events. A number of significant climate events occur through the 13 Myr study interval, including named transient events marked by isotopic excursions and identified on Figures 1 and 3, with further details provided in Extended Data Table 2. These are mainly global warming hyperthermal events identified by carbon and oxygen isotope excursions and associated deep-sea carbonate dissolution. Events I2, I1, H2, H1 and the PETM were recognised at ODP Site 1209 by examination of benthic and bulk carbon isotope values and magnetic susceptibility data, following refs 21 and 32. The PETM was also identified in benthic carbon isotope values and XRF Fe intensity data, following refs 35, 48. The Palaeocene Carbon Isotope Maximum (PCIM); Early Late Palaeocene Event (ELPE); Latest Danian Event (LDE) and the K/Pg boundary were identified in benthic carbon isotope values and XRF Fe intensity data[48], and the positions of the PCIM and LDE were verified against records from ODP Site 1262[49]. The Lower C29n and Dan-C2 events are not clear in the benthic carbon isotope data at ODP Site 1209[48], but were identified following ref 50, who suggest that the peaks in magnetic susceptibility[51] and XRF Fe intensity[35] identified as Pa2 and Pa1 by ref 35 correlate with the Lower C29n and Dan-C2 events, respectively. The position of the Dan-C2 is consistent with estimates for the timing of this event[34,52].

Relationships between variance and carbon isotope excursion magnitude. For each climate event we use the carbon isotope excursion (CIE) magnitude as a proxy for the level of environmental perturbation, as illustrated by the scaling of temperature change with CIE size for several of the Eocene hyperthermals[53]. For the purposes of comparing environmental perturbation and Σ_{CV} (Fig. 2), we plot magnitude of CIE using a combination of size of excursion as recorded at ODP Site 1209 and the magnitude of excursion estimated from

468   published bulk carbon isotope data at globally distributed sites (Extended Data Table 2). We
469   used the maximum recorded excursion, except where this was inconsistent with other
470   available data. As well as values from bulk carbon isotope data (consistent with ref 21), we
471   took into account available benthic CIE values, which are arguably preferable for resolving
472   global signals[54]. The value of carbon isotopes used for plotting non-event Σ_{CV} data points in
473   Figure 2 uses the deviation of the carbon isotope value from the detrended running average
474   (using an 11-point running average through non-event-only values), for a data-point every
475   ~150 kyr between climatic events. We regressed first differences in Σ_{CV} and first differences
476   in CIE magnitude (Fig. 2b) to statistically explore the relationship between community
477   stability and climate change across this 13-million-year interval, using a generalised least
478   squares framework (gls function in the nlme library in R) that applies best-fit models that
479   incorporate heteroscedastic (non-constant variance with the mean) and temporally auto-
480   correlated (time-series) errors.

481   **Milestones (Figure 3).** *Biological pump reboot (0.30 Myr) and recovery (1.77 Myr)*: Carbon
482   isotope records of benthic and planktonic foraminifera from Walvis Ridge (southern
483   Atlantic), adjusted to account for vital effects and ecology, show a crash in surface- to deep-
484   water carbon-isotope gradients at the mass extinction level and indicate that transfer of
485   organic matter to the deep-sea via the biological pump was severely perturbed[9]. These
486   records show that vertical gradients were close to zero for the initial 0.3 Myr after the
487   extinction, then slowly increased to attain pre-extinction levels at around 1.77 Myr. This is
488   interpreted as evidence that the duration of weakened biological pumping was no longer than
489   1.77 Myrs[9], providing an estimate for full biological pump recovery. *Photosymbiosis and*
490   *depth partitioning in planktonic foraminifera (2.5 Myr)*: Based on reconstructions of the
491   palaeoecology of planktonic foraminifera using the oxygen and carbon stable isotopes of their
492   shells, the appearance of photosymbiosis and expansion of depth partitioning both occur
493   around 2.5 Myr after the mass extinction[9,55]. *Appearance of oligotrophic coccolithophores*
494   *(3.5 Myr)*: The first appearance of early fasciculiths and sphenoliths represent the earliest
495   representatives of the Discoasterales group, which is largely characterized by oligotrophic
496   taxa (e.g., ref 28). The earliest representatives, *Fasciculithus magnus* and *F. magnicordis*,
497   appear at ~63 Myr ago (herein; ref 56) with other fasciculiths and sphenoliths following soon
498   after (62.13 and 61.98 Myr ago, according to ref 43).

499   **Selected taxonomic notes.** *Praeprinsius*: used here to include very small (<3µm) circular to
500   subcircular specimens of *Praeprinsius tenuiculum*. *Praeprinsius* is considered a synonym of
501   *Prinsius* by some, but we consider these groups to be morphologically distinct. *Fasciculithus*:
502   We use 'early fasciculiths' to include specimens that some may now identify as
503   *Gomphiolithus*, *Diantholitha*, and *Lithoptychius* (e.g., refs 56,58,59), while our main
504   '*Fasciculithus*' group includes taxa that have been consistently classified within this genus,
505   e.g., *F. involutus* and *F. tympaniformis*. *Sphenoliths*: The earliest specimens of the genus
506   *Sphenolithus* (e.g., refs 56,60) are highly variable and we distinguish between the earliest
507   incoming specimens (termed 'early sphenoliths') and the main generic group '*Sphenolithus*',
508   which includes *S. primus/moriformis* and *S. anarrhopus*.

509

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649   **Author contributions** S.J.G., P.R.B. and A.R. conceived and designed the study. S.A.A.
650   developed the methodology and performed the majority of data collection. S.A.A. and S.J.G.
651   performed the data analyses. P.R.B., R.M.S., H.K. and A.R. contributed to data collection,
652   analysis and interpretation. S.J.G. and P.R.B. wrote the manuscript and A.R., S.A.A. and
653   R.M.S. participated in manuscript writing and editing.

654   **Author Information** Reprints and permissions information is available at
655   www.nature.com/reprints. The authors declare no competing interests. Correspondence and
656   requests for materials should be addressed to S.A.A. (sarah.alvarez@unigib.edu.gi) or S.J.G.
657   (sxg@noc.soton.ac.uk).

658   **Data availability** The datasets generated or analysed during this study are included in the
659   published article, linked directly to figures 1, 2 and 3.

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Extended data figures:
663   **Extended Data Figure 1. Location of ODP Site 1209 (black star) with respect to model**
664   **simulated late Cretaceous major ocean current and circulation patterns. a**, Barotropic
665   streamfunction simulated in a late Cretaceous configuration of the *c*GENIE Earth system
666   model[47]. **b**, Surface ocean current field (black arrows) for the same circulation state as (**a**)
667   overlain on annual average ocean surface temperature (colours). Scale for current vectors on
668   the right, along with a truncated temperature scale to highlight distribution of comparable
669   temperature regimes. Red arrows illustrate inferred flow paths relevant to the position of
670   ODP Site 1209 (marked by a star).

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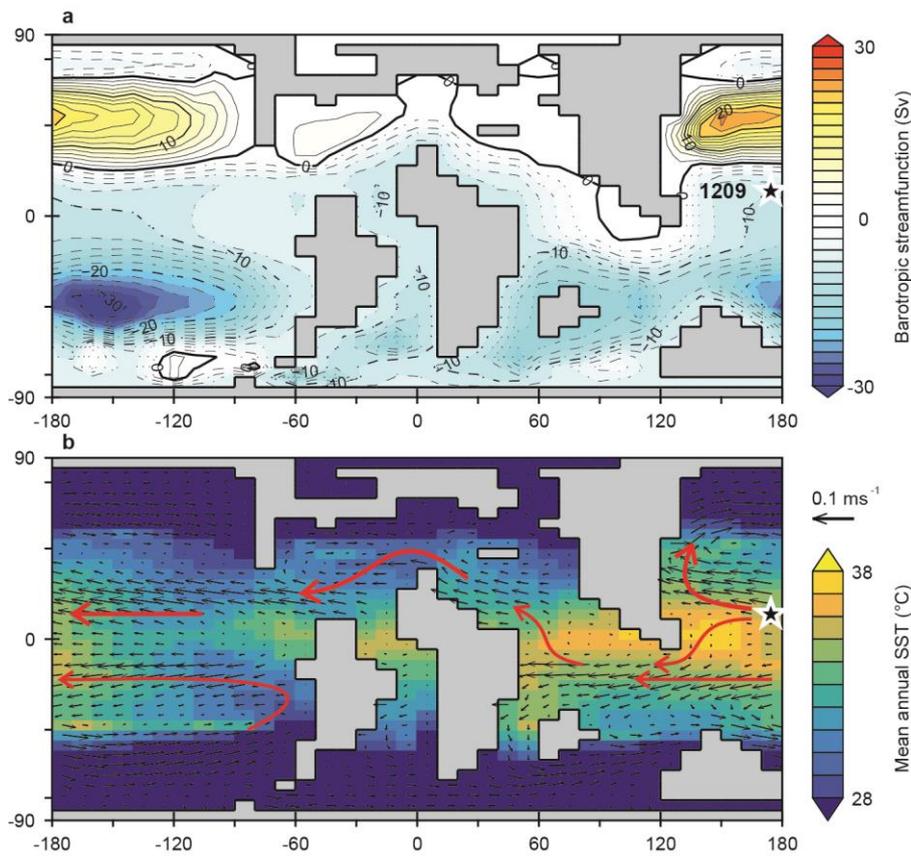
Extended Data Figure 2. Comparison of community structure metrics. Downcore plots
of (**a**) Σ_{CV}, (**b**) Bray-Curtis dissimilarity (BC), (**d**) Simpson's index (SI, grey dashed lines,
150 kyr moving average – black line) and the variance (150 kyr window) in the SI (**c**).
Vertical grey lines on **a** and **b** show the level of background inferred from rank order plots of
these data. All four metrics (Σ_{CV}, BC, SI and SI-variance) show volatility distinction between
early Danian Regime 1 (n = 137 data points) and Regime 2 (the rest of the record, n = 861
data points), e.g., the Wilcoxon Rank Sum value for the Simpson's record = 46646, p<0.001
on first differences, with 95% confidence limits of -0.013, -0.006. A W value of zero would
support a null hypothesis. The test was two-sided. SI shows a diversity minimum in the
earliest Danian and then a rapid increase and steady long-term trend towards more diverse,
more even communities, but with high variability in the early Danian. This SI fluctuation, as
recorded by the record's variance (**c**) shows similar patterns to BC and Σ_{CV} with high
variance in the early Danian before dropping down. SI variance also shows high background
fluctuations and a sustained rise in amplitude of fluctuations around the PCIM isotope shift,
reflecting oligotroph diversification, which the SI shows strongly due to its higher sensitivity
to rare taxa. In effect, metric sensitivity to taxic richness and rare taxa increases from panel **a**
to **c** (from abundance variance to diversity variance). Note – SI can only be performed on full
assemblage data and therefore the record only extends up to 55.5 Myr ago.
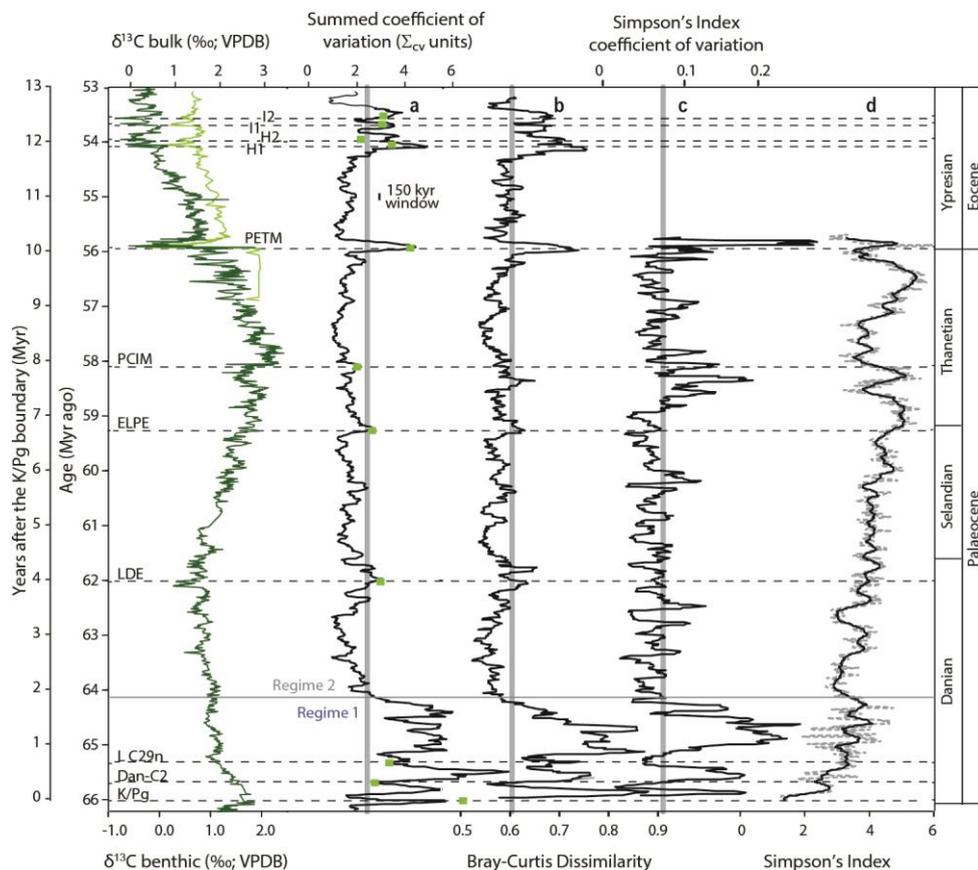
Extended Data Figure 3. Relative abundance of key nannoplankton groups and abundance of reworked specimens per 100 nannofossils. Relative abundance of coccoliths from all groups included in the Σ_{CV} metric are shown, coloured according to clade (as per Fig. 1b) and ordered by stratigraphic appearance. Cretaceous survivor taxa were counted as individual species but have been grouped together here, comprising mostly *Zeugrhabdotus* with lower abundances of *Cyclagelosphaera*, *Markalius* and *Neocrepidolithus*.
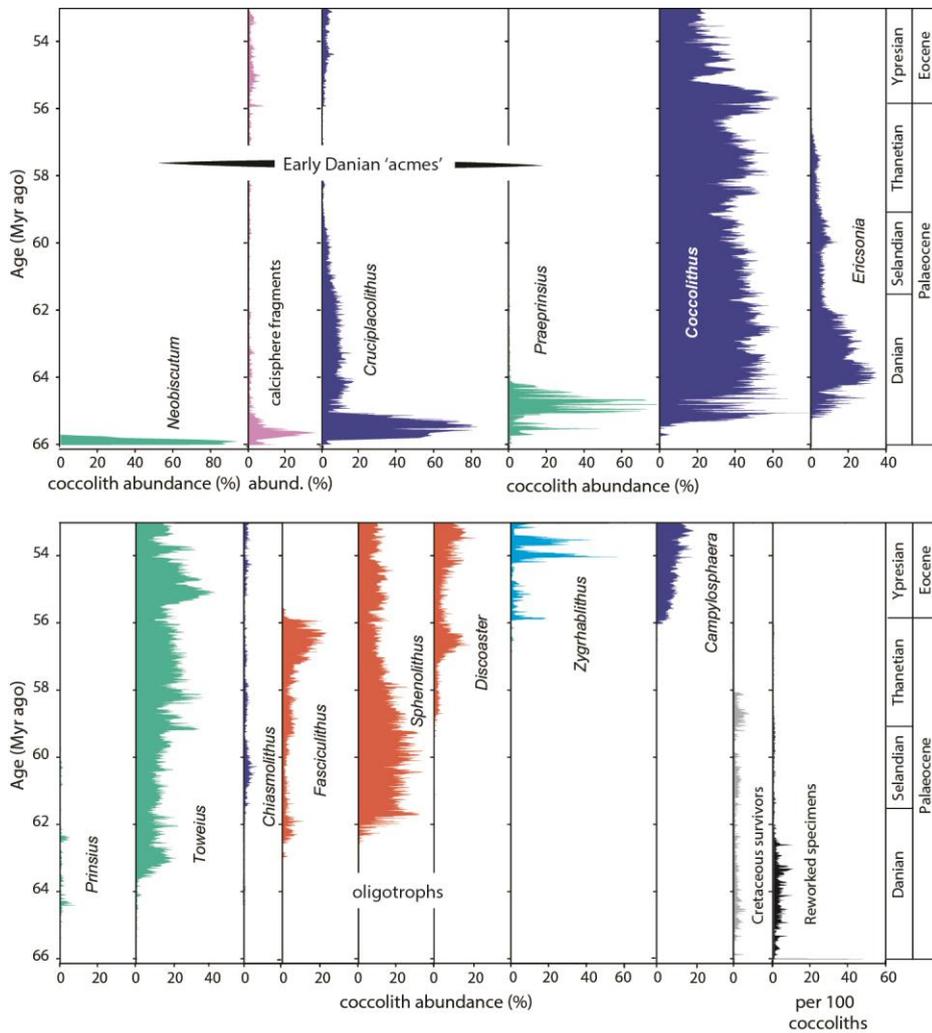
704 **Extended Data Figure 4. Calcareous nannoplankton across the K/Pg boundary.**
705 Stratigraphic distribution of significant species grouped as incoming (brown), survivor
706 (green) or disappearing taxa (blue). A subset of Cretaceous taxa are shown, with latest
707 Maastrichtian diversity for families shown alongside number of survivors. Gradualistic
708 evolutionary transitions indicated by close spacing and arrows indicate genus-level
709 transitions. The nannoplankton data are primarily from our work but are largely consistent
710 with published sources (e.g., refs 10,15,16,37,61). Diversity and cell-volume records from
711 Figure 3. *Cp*. = *Cruciplacolithus*, Dan-C2, L C29n = hyperthermals, LDE = late Danian
712 event, *Neobisc*. = *Neobiscutum*, NP = nannofossil biozone, *Prae*. = *Praeprinsius*.

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Extended Data Figure 6. Phylogenetic models for the dominant Paleocene
731 **nannoplankton.** Models range from a standard genus-level stratophenetic tree (**a**) through
732 two successively conservative scenarios (**b**, **c**) grouping closely-related taxa, i.e., recently
733 diverged taxa based on morphological and stratigraphic range data. Nannoplankton taxonomy
734 is primarily based on the morphology and crystallographic ultrastructure of exoskeletal
735 coccoliths but the addition of genetic data for modern taxa has confirmed that this approach is
736 robust[62,63,64]. Evolutionary models are stratophenetic because we have high-quality
737 stratigraphic information but lack the range of meaningful homologous morphological
738 characters to allow a cladistic analysis. **a**, genus-level phylogeny based on an extensive
739 species-level stratophenetic tree. **b** and **c** are different ancestry options used to test for
740 artefacts and sensitivity in variance/dissimilarity that may result from equal weighting of
741 closely-related versus more distantly-related taxa. **b**, ancestry model option 1 is highly
742 conservative and merges major sub-family groups (shown by shaded boxes) about five nodes
743 shown by black circles. **c**, ancestry model option 2 merges the most closely-related genera
744 (shaded boxes) about eight nodes.

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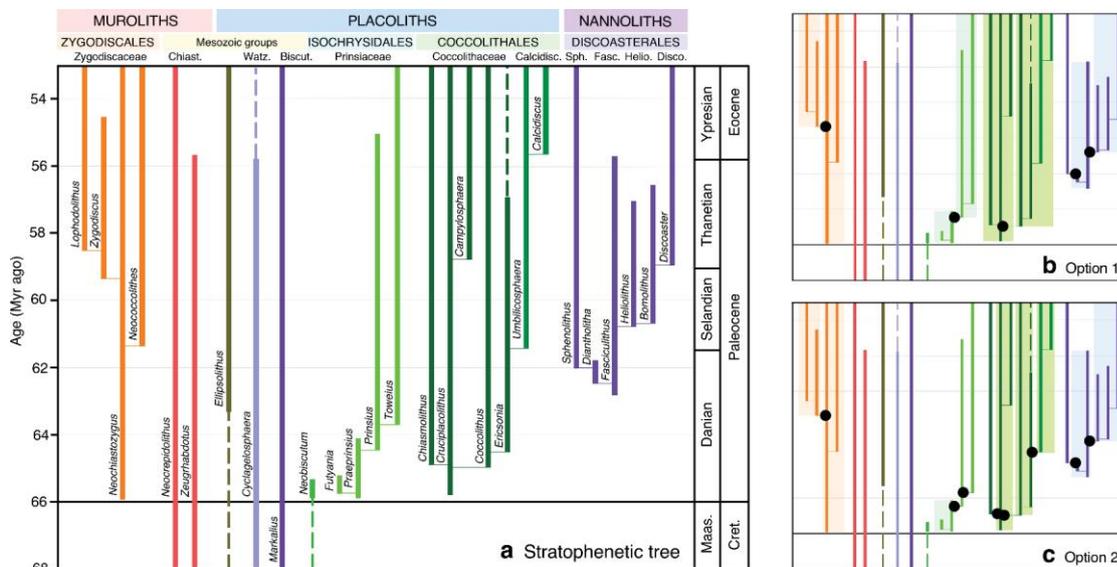
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748 **Extended Data Figure 7. Impact of 'ancestry' on (a) summed coefficient of variability**
749 **(ΣCV) and (b) Bray-Curtis dissimilarity (BC).** Analyses of the dataset applying two
750 additional models of shared ancestry using the reconstructed genus-level stratophenetic tree
751 in Extended Data Figure 6a. In red, the original analysis giving each genus equal. In grey,
752 analysis of the conservative ancestry model that merges genera into major sub-family groups
753 (ancestry model option 1, Extended Data Fig. 6b). In black, analysis of the moderately
754 conservative ancestry model option 2 (Extended Data Fig. 6c) which merges the most
755 closely-related genera. BC displays very little sensitivity to varying the taxonomic
756 hierarchies. ΣCV displays some sensitivity, particularly at the Late Danian Event (around 62
757 Myrs ago) but the main patterns are retained between the original and option 2. Some
758 variance is lost in the less realistic option 1 analysis, where grouping of key genera that lie in
759 the same families dampens the variance, in particular, in the early Danian. However, the early
760 Danian variance values still remain anomalously high compared to the rest of the record.

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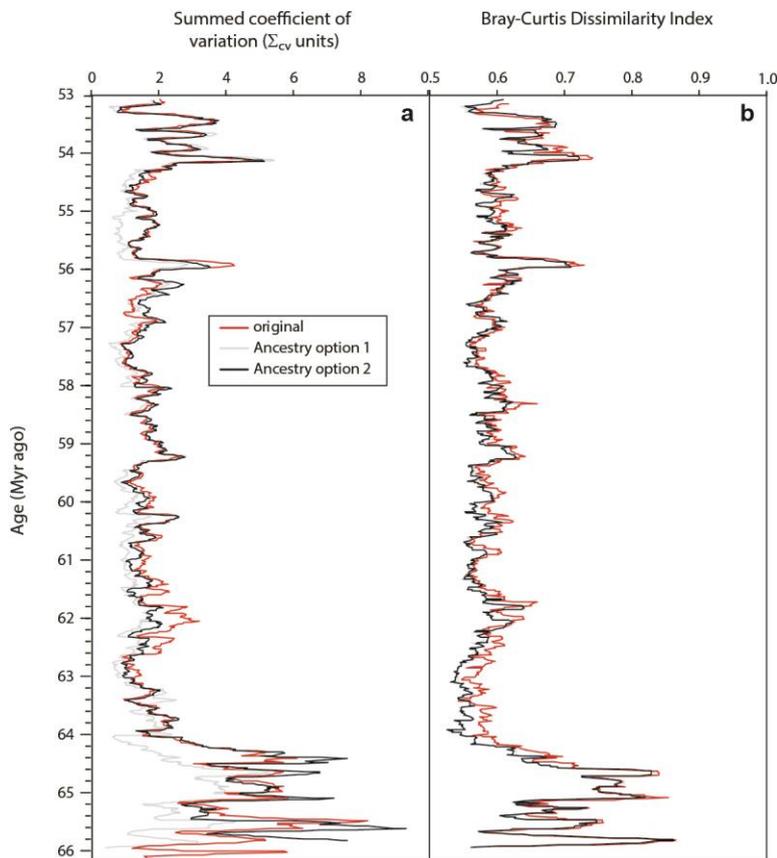
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764 **Extended Data Table 1. Summary of main biometric lith and cell parameters measured**
765 **and reconstructed.** C_N is the number of coccoliths per cell, Θ is cell diameter, and C_L is lith
766 length. Sites referred to include ODP Site 1209 and IODP Sites 1403 and 1407. 'Pg
767 coccospheres' refers to new coccosphere measurements for the Palaeogene. SEM images of
768 published coccospheres are all from refs 44,45.

769

Clade	Taxon	Lith number (C_N)	Cell size (Θ, μm)	Cell volume (μm³)	Source
Cretaceous survivors	*Neocrepidolithus*	32.5	16.5	2352	Ref. 46
	Zeugrhabdotus	32.5	16.5	2352	Ref. 46
	Markalius	12	8.3	297	Pg coccospheres
	Cyclagelosphaera	12	7.9	259	C_N from published SEM images; Θ estimated from lith measurements at Sites 1209, 1403 and published coccosphere images. Geometry consistent with Pg coccospheres
Coccolithales	*Chiasmolithus*	9	11.0	698	Pg coccospheres
	Coccolithus	13	7.0-9.7	180-478	C_N from Pg coccospheres; Θ change through Danian estimated from lith measurements at Sites 1209 and 1403 using geometric relationship from Pg coccospheres
	Cruciplacolithus (small)	20	4.2-8.0	39-268	C_N and Θ from Pg coccospheres and published coccosphere images; Θ change through Danian estimated from lith measurements from Sites 1209 and 1403 using geometric relationship from Pg coccospheres.
	Cruciplacolithus (large)	13	6.6-11.5	151-796	As for *Cruciplacolithus* (small), but considered to be more like *Chiasmolithus*
	Ericsonia	13	7.6	226	As for *Coccolithus*
Isochrysidales	*Neobiscutum*	9	3.0	14	Direct measurements of Danian coccospheres and estimates of Θ based on lith measurements from Sites 1209, 1403 and 1406.
	Praeprinsius	18	3.8-5.2	29-74	Direct measurements of Danian coccospheres and estimates of Θ change through Danian based on lith measurements from Sites 1209, 1403 and 1406.
	Futyania	50	8.5	322	Pg coccospheres and published coccosphere images
	Prinsius	20	4.0-5.5	34-87	Direct measurements of Danian coccospheres and estimates of Θ change through Danian based on lith measurements from Sites 1209, 1403 and 1406.
	Toweius	7	4.7	31	C_N from Pg coccospheres; Θ estimated from lith measurements from Sites 1209 and 1403 using geometric relationship from Pg coccospheres.
Zygodiscales	*Neochiastozygus*	32.5	16.5	2352	Ref. 46
Discoasterales	*Fasciculithus, Sphenolithus*	42	21.7	5350	Ref. 46
Incertae	*Biantholithus*	13	13.7	1337	Pg coccospheres
Non-nannofossil	Calcisphere fragments	16	20.0	4189	Pg coccospheres

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772 **Extended Data Table 2. Carbon isotope excursion events.** Columns provide event
773 nomenclature, depth in core at Site 1209, age and estimated size of the CIE. Values in
774 parentheses show the range of CIEs from the literature cited and the value in bold is the size
775 of CIE used in Figure 2. Event nomenclature follows references given in the Methods, depths
776 (rmcd – revised metres composite depth) use the revised depth splice of ref 33 and the ages
777 use the age model from ref 32.

778

Event	Depth (rmcd, splice)	Age (Myrs ago)	Size of CIE (‰)	References
I2	210.02	53.55	**0.48** [0.1 – 0.6]	21,65,66.
I1	210.60	53.67	**0.65** [0.5 – 0.7]	21,65,66.
H2	211.83	53.95	**0.49** [0.2 – 0.6]	21,51,65,66.
H1	212.48	54.05	**1.5** [0.6 – 1.6]	21,51,65–67.
PETM	218.00	55.93	**3.0** [2.4 – 3]	68,69.
PCIM	229.94	58.10	1.0	48,49.
ELPE	235.00	59.27	0.75	48,49,72.
LDE	247.69	62.03	1.0	48,71–76.
L C29n	258.83	65.34	0.7	50,77.
Dan C2	260.11	65.71	1.3	50,77,78.

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