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### Authors

Birch, Heather  
Schmidt, Daniela N  
Coxall, Helen K  
et al.

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**Author for correspondence:**

Heather Birch

e-mail: [heather.birch@bristol.ac.uk](mailto:heather.birch@bristol.ac.uk)

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# Ecosystem function after the K/Pg extinction: decoupling of marine carbon pump and diversity

Heather Birch<sup>1</sup>, Daniela N. Schmidt<sup>1</sup>, Helen K. Coxall<sup>2</sup>,  
Dick Kroon<sup>3</sup> and Andy Ridgwell<sup>4</sup>

<sup>1</sup>School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

<sup>2</sup>Department of Geological Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

<sup>3</sup>School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FE, UK

<sup>4</sup>Department of Earth and Planetary Sciences, University of California Riverside, Riverside, CA 92521, USA

HB, 0000-0003-1515-0645; DNS, 0000-0001-8419-2721

The ocean biological pump is the mechanism by which carbon and nutrients are transported to depth. As such, the biological pump is critical in the partitioning of carbon dioxide between the ocean and atmosphere, and the rate at which that carbon can be sequestered through burial in marine sediments. How the structure and function of planktic ecosystems in the ocean govern the strength and efficiency of the biological pump and its resilience to disruption are poorly understood. The aftermath of the impact at the Cretaceous/Palaeogene (K/Pg) boundary provides an ideal opportunity to address these questions as both the biological pump and marine plankton size and diversity were fundamentally disrupted. The excellent fossil record of planktic foraminifera as indicators of pelagic-biotic recovery combined with carbon isotope records tracing biological pump behaviour, show that the recovery of ecological traits (diversity, size and photosymbiosis) occurred much later (approx. 4.3 Ma) than biological pump recovery (approx. 1.8 Ma). We interpret this decoupling of diversity and the biological pump as an indication that ecosystem function had sufficiently recovered to drive an effective biological pump, at least regionally in the South Atlantic.

## 1. Introduction

Currently, the oceans provide about half of the global net primary production (NPP), approximately  $48.5 \text{ Pg C yr}^{-1}$  [1]. The fate of most primary production in the ocean is remineralization and rapid recycling of nutrients and  $\text{CO}_2$  in the upper ocean [2]. On average, only 20% [3] is exported in the form of particulate organic matter into the ocean interior. There, approximately 97–99% [4] is remineralized, but now spatially separated from the ocean surface and atmosphere. A return to the surface from the deep ocean depends on the much slower action of ocean circulation and upwelling. A small fraction of particulate organic matter and hence carbon also escapes the ocean-atmosphere system and is buried in marine sediments, helping regulate atmospheric  $p\text{CO}_2$  on geological time scales. This dynamical biogeochemical partitioning between ocean surface and interior, particularly of carbon, is known as the marine ‘biological pump’. This process influences not only nutrient availability and primary production, but also atmospheric  $p\text{CO}_2$ , and hence climate, among the fundamental functions of the marine pelagic ecosystems.

The strength (magnitude) and the efficiency (remineralisation depth) of organic matter transfer by the biological pump is highly variable [5]. This variability is largely a result of differences in phytoplankton, zooplankton and microbial communities and food web structures [4,5]. For example, the proportion of large cells within the phytoplankton community influences the flux of particulate organic carbon (POC) [6], while the type and nature of zooplankton feeding can lead to an increase or decrease in the sinking rate of organic matter [4].

Understanding the controls on both primary production as well as the efficiency of transfer of carbon to the ocean floor is hence essential for an understanding of the regulation of  $p\text{CO}_2$  and climate.

Model projections show marine primary production decreasing globally due to climate change [7,8] particularly in the tropics and the North Atlantic, though uncertainties are high [7,9]. Environmental changes in temperature and  $\text{CO}_2$  concentration impact the ratio of calcifiers to non-calcifiers (potentially changing the composition and hence sinking rate of particles), as well as the proportion and size of plankton and grazers [10–13]. Modelling studies reveal that under projected future climate change, the decrease in phytoplankton size exerts the largest influence on decreasing POC flux out of the surface ocean, whereas changes in zooplankton communities are important in the subsurface ocean [14]. Assessing these interactions is essential for understanding the critical elements in, and the resilience of, the biological pump to perturbations. Observational time series are not long enough to reject or support these projections [15]. The longer perspective of the fossil record, however, could fill this gap as well as providing crucial information to address potential impacts of marine extinctions, given the anthropogenic effect that humans are having on Earth's processes in the wake of a potential 6th mass extinction [16,17].

As isotopically light carbon ( $^{12}\text{C}$ )  $-\text{CO}_2$  is preferentially taken up during primary productivity in the surface ocean, the carbonate shells mineralized by planktic foraminifera are relatively enriched in  $^{13}\text{C}$  compared to the organisms that precipitate carbonate in the deep ocean (e.g. benthic foraminifera), where organic matter is remineralized releasing  $^{12}\text{C}$ , resulting in a vertical carbon isotope ( $\delta^{13}\text{C}$ ) gradient [18]. The greater the surface-deep  $\delta^{13}\text{C}$  difference the more efficient the biological pump. This signal of biological pump efficiency (which differs from strength, see [19] for details) is recorded in the shells of foraminifera and combined in the geological record with information on the ecological composition of planktic ecosystems.

The Cretaceous/Palaeogene (K/Pg, 66.02 Ma) mass extinction [20] was the most important extinction in the evolutionary history of modern plankton [21] and provides an excellent opportunity to understand how a severe perturbation to the planktic ecosystem affects the biological pump. Based on interpretations of a surface to deep ocean  $\delta^{13}\text{C}$  gradient of near zero [22], it has been suggested that the extinction led to a near complete shutdown of the biological pump, with a recovery time of several millions of years [22–24]. However, a lack of extinction within benthic communities, which depend on surface-exported food supplies, challenges this interpretation (see [22]). While some proxies, such as biogenic barium [25], suggest spatial heterogeneity in productivity between the major ocean basins and open ocean versus shelf environments, the  $\delta^{13}\text{C}$  signal is a global phenomenon [23,26]. Previous studies have focused on either the recovery of the marine biological pump [22,24,27] or the pelagic biota [28,29]. Few studies have tried to establish the link between the two [30–32].

While ideally the whole ecosystem would be interrogated, most pelagic organisms do not preserve in the fossil record [33]. Fortunately, two important autotrophic and heterotrophic components have excellent fossil records i.e. calcareous nannoplankton (haptophyte algae) and planktic foraminifera (shell-building micro-zooplankton) that provide representative

signals of the pelagic ecosystem. Differences in rates of recovery of the biological pump, plankton diversity and size are apparent in the fossil record [30,31,34–37]. Recently, post-K/Pg ecosystem recovery, assessed via community stability history of nannofossils, has been linked to a return of the biological pump in the Pacific, approximately 1.8 Myr years after the event [31]. Here, we assess whether the marine biological pump drove ecological changes, or, whether the recovery of the biological pump was itself contingent on pelagic community recovery (diversity, size) to fulfil their ecological function. We explore whether ecosystem function (i.e. the contribution of marine plankton in the regulation of the global carbon cycle) depends on diversity to be re-established. Specifically, we question how important diversity recovery at higher trophic levels is for the efficiency of the biological pump. Moreover, did the evolution of certain traits in plankton, such as body size and photosynthesis, drive the restoration in biological pump efficiency, or do certain environmental and ecological thresholds need to be met for these traits to be established? Here, we focus on planktic foraminifera, which benefit from a well-established understanding of both modern and paleo-diversity and ecological preferences [38], and several methods for documenting the evolution of body size [35,39].

## 2. Method

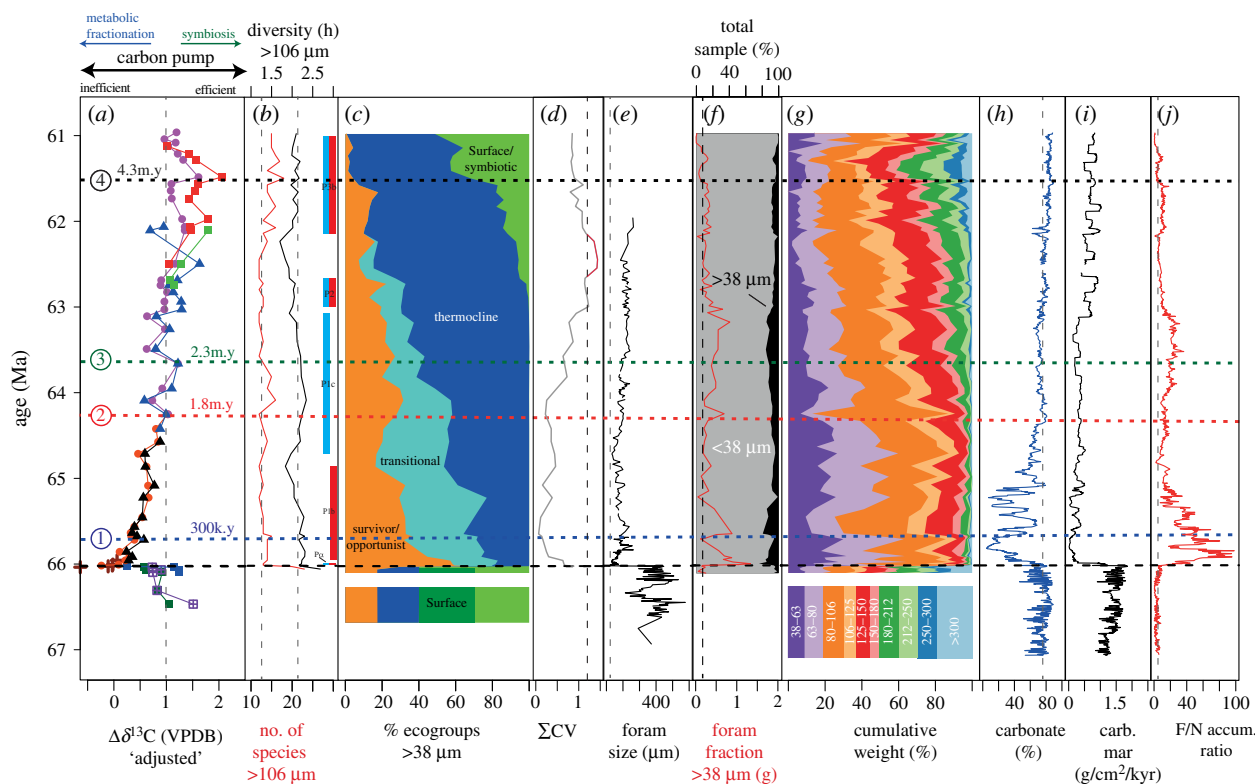
The K/Pg event is captured in Ocean Drilling Program (ODP) Site 1262, Walvis Ridge ( $27^{\circ}11.15'\text{S}$  and  $1^{\circ}34.62'\text{E}$ ; electronic supplementary material, figure S1). The K/Pg boundary occurs at approximately 216.6 m composite depth (mcd), calibrated to 66.02 Ma on an astronomically tuned time scale [40]. Consistent preservation of calcitic microfossils suggests deposition above the carbonate compensation depth throughout the K/Pg interval [41].

Core samples were washed over a  $38\ \mu\text{m}$  sieve and dried in an oven at  $40^{\circ}\text{C}$ . Planktic foraminifera species abundance counts were made on 49 samples. Taxonomy follows the Palaeocene Atlas [42] and Cretaceous chapters of *Plankton stratigraphy* [43]. The summed coefficient of variation metric ( $\Sigma\text{CV}$ ), which quantifies the level of stability, was calculated per sample for the five designated ecogroups, clusters of species sharing similar ecologies, following the method of [44], without the SiZer smoother step, as in [31].  $\Sigma\text{CV}$  was chosen as it is independent of taxonomic composition. Separated sieved size fractions (electronic supplementary material, table S1) were weighed in 94 samples. Samples were weighed using an A & D semi-microbalance (standard deviation of 0.1 mg). The species/genera counts were assigned to one of five ecogroup categories for the Palaeocene and one of four categories for the Cretaceous (electronic supplementary material, table S2).

A representative split of 356 washed samples (greater than  $38\ \mu\text{m}$ ) was analysed for foraminifera size. Size parameters of randomly oriented foraminifera were measured using a Malvern Mastersizer laser granulometer. The maximum diameter of the object was chosen as the most suitable size estimator because it is least affected by random orientation. The 90th percentile of the maximum diameter (or D90) was used to describe these strongly skewed distributions.

## 3. Results

Our data show that overall planktic foraminifera diversity remained low compared to pre-extinction assemblages for approximately 4.8 Myr post-extinction (figure 1b). Test size dropped dramatically from approximately 400 to  $150\ \mu\text{m}$  at



**Figure 1.** Multiproxy K/Pg datasets from Site 1262. (a) Adjusted stable carbon isotope ( $\delta^{13}\text{C}$ ) differences between planktic and benthic foraminifera [22]. (b) Shannon diversity of planktic foraminifera greater than  $106\ \mu\text{m}$  (black line) and total number of species greater than  $106\ \mu\text{m}$  (red line). Blue and red bars indicate intervals of enhanced planktic foraminifera species origination and extinction [34], respectively, and vertical dashed lines show minimum K/Pg value. (c) Relative abundance (%) of Palaeocene planktic foraminifer ecogroups. (d) Summed coefficient of variation metric ( $\Sigma\text{CV}$ ). (e) 90th percentile foraminifera size ( $\mu\text{m}$ ) [35]. (f) weight contribution (g) of the foraminiferal fraction (i.e. coarse fraction greater than  $38\ \mu\text{m}$ ) to the bulk sediment. (g) Planktic foraminifera test size spectrum shown as cumulative weight % (g) of size fractions. (h–j) The % carbonate, carbonate accumulation rate and foraminifera/nannofossil accumulation ratio [45]. Ages are based on the tuning of the records to La2011 [40]. Horizontal black dashed line represents the K/Pg boundary and coloured numbered lines relate to significant steps in the recovery process; 1—initial partial recovery of the surface-to-deep carbon gradients, 2—‘full’ carbon gradient recovery, 3—appearance of photosymbiotic ecologies [22,46] and 4—‘full’ planktic biotic recovery. (Online version in colour.)

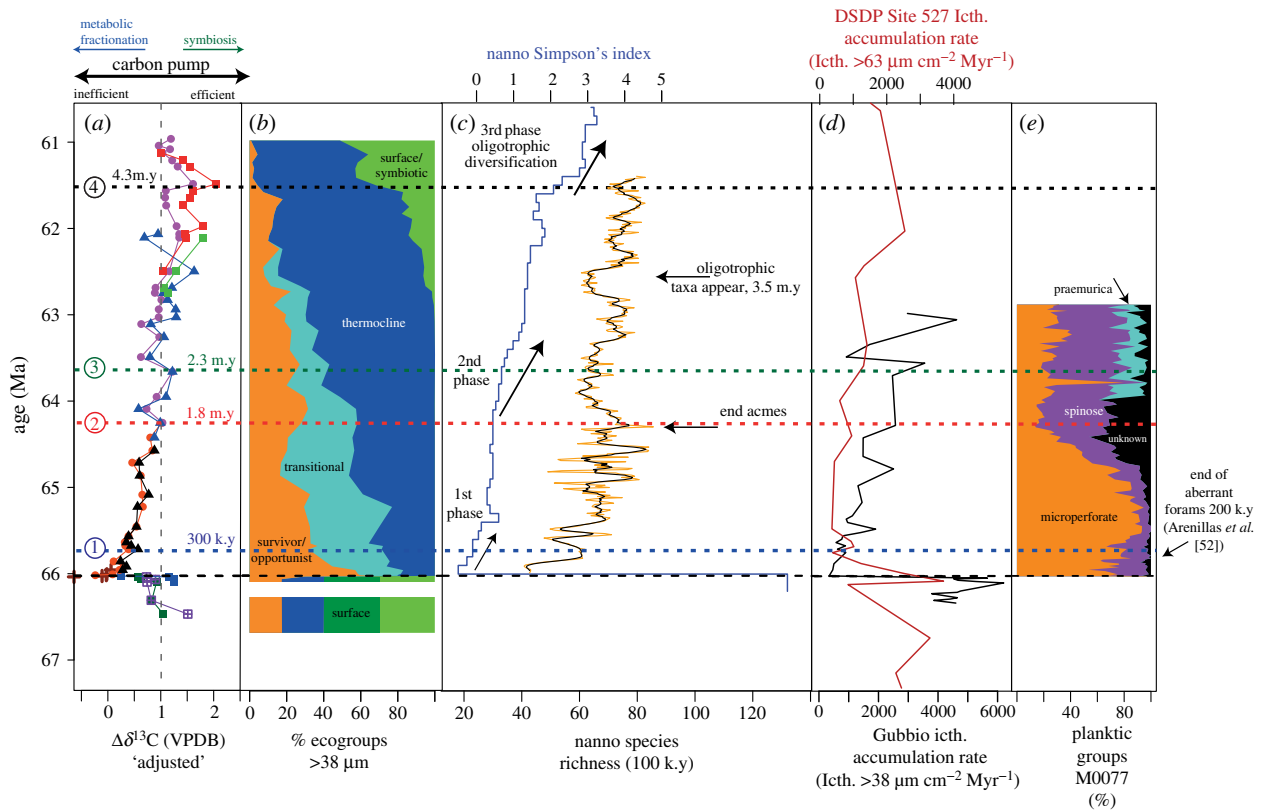
the K/Pg and small size persists throughout the studied interval (figure 1e). Linked to this, the relative proportion of particles greater than  $38\ \mu\text{m}$  increased indicating a higher contribution of planktic foraminifera to bulk carbonate (figure 1f). Dividing the greater than  $38\ \mu\text{m}$  foraminiferal fraction further (electronic supplementary material, table S1) shows that most size classes contributed roughly equally to the assemblage in the Cretaceous (approx. 5–15%). After the K/Pg boundary, approximately 75% of the total foraminiferal fraction were in the size fraction below  $106\ \mu\text{m}$  (figure 1g). Consequently, carbonate accumulation rates dropped strongly, enhanced by the mass extinction of calcareous nannofossils, which typically contributed 80–90% of the bulk dry weight before the extinction (figure 1h,i, respectively). However, the abundance of small opportunistic planktic foraminifera increased (figure 1g) and resulted in an increased contribution of foraminifers to bulk carbonate (figure 1j). Between the partial and full recovery in the marine biological pump (300 kyr to 1.8 Myr later; line 1 to 2) many of the sedimentary parameters (% carbonate, F/N ratio and foram fraction) began to stabilize. Alpha diversity increased after approximately 1.8 Ma and approximately 4 Ma, indicating that originations exceeded extinctions for a brief period (figure 1b). These diversity increases were associated with minor increases in foraminifera size (figure 1e).

The survivor and opportunistic species dominated the initial recovery interval (approx. 100 ka). These were followed

by ‘transitional’ taxa (figure 1c) whose early representatives were deep dwellers while descendent species migrated to surface waters and/or became symbiotic. The transitional taxa declined and were replaced by thermocline species around 1 Ma (figure 1c). A surface/symbiotic group appeared approximately 3 Myr later (figure 1c) when size spectra widened and small taxa and individuals lost their dominance (to approx. 50%, figure 1g). The balance between the relative contribution of the two carbonate producing groups (figure 1f,j) returned to pre-extinction levels also by approximately 3 Ma.  $\Sigma\text{CV}$  shows a small peak (approx. 3.5 Ma) above background variation (electronic supplementary material, figure S3), which coincides with the decline and extinction of the transitional taxa and the early radiation of the surface/symbiotic group. This group only became an important component of the assemblages approximately 4.3 Myr after the extinction, when assemblage ecological characteristics were restored but with completely different species. While size classes diversified, they did not reach the overall sizes of the Cretaceous.

## 4. Discussion

The impact of an asteroid at the K/Pg had devastating effects on Earth’s fauna and flora and created environmental instability [20]. Extreme temperature changes, reduced pH, heavy metal loading, stratification and increased nutrients



**Figure 2.** Multiproxy K/Pg datasets. (a) Adjusted stable carbon isotope ( $\delta^{13}\text{C}$ ) differences between planktic and benthic foraminifera for Site 1262 (see [22]). (b) Relative abundance (%) of Palaeocene planktic foraminifer ecogroups for Site 1262. (c) Nannoplankton community variance; Simpson's Diversity Index ODP Site 1209, Global species richness from [31]. (d) Ichthyolith accumulation rates; Tethys Sea (Gubbio, Italy; Icth.  $>38 \mu\text{m}/\text{cm}^2 \text{Myr}^{-1}$ ) from [55] and Walvis Ridge, DSDP Site 527 in the South Atlantic (Icth.  $>63 \mu\text{m} \text{cm}^{-2} \text{Myr}^{-1}$ ) from [56]. (e) Percentage planktic groups from Site M0077 [37]. Ages are based on the tuning of the records to the latest orbital solution La2011, [40]. Horizontal black dashed line represents the K/Pg boundary and coloured numbered lines relate to significant steps in the recovery process; 1—initial partial recovery of the surface-to-deep carbon gradients, 2—'full' carbon gradient recovery, 3—appearance of photosymbiotic ecologies (see [22] for details) and 4—'full' planktic biotic recovery. (Online version in colour.)

are all thought to have played a part in the initial extinction and dictated what organisms survived [20,32,47]. Environmental conditions feedback on the diversity and abundance of marine organisms [48–50] and thereby change the fixation and export of carbon and utilization of nutrients.

As marine ecospace was re-created [28,36,51], rates of evolutionary turnover were far above typical background rates [34]. Small, opportunistic planktic foraminifera dominate the early Danian [29] and a high frequency of morphological abnormalities in Tunisian planktic foraminifera has been linked to severe environmental instability [52]. Successive acmes of opportunistic, eutrophic calcareous nanofossils are attributed to high-nutrient loads [31,37], as are increases in high-nutrient, opportunistic dinoflagellates, indicative of eutrophication in marginal settings [53]. Blooms of neritic opportunistic dinoflagellates declined by the end of biozone P1a [53], approximately 50 kyr after the extinction. Planktic foraminiferal abnormalities reduced to background levels 200 kyr after the K/Pg [52]. Disappearance of these bloom forming, high-nutrient taxa suggests that the reduction of nutrient levels in marginal surface waters predates the initial return of export productivity observed in the open ocean (line 1, figure 1a) [22] supporting suggestions that neritic and marginal marine environments recover quicker ( $<10 \text{ kyr}$ ) than open ocean environments [54]. The microperforate group (which is similar to our opportunistic/survivor group) at the shallow water impact Site M0077 [37] declined in abundance from approximately 1.2 Ma ending near the return of the biological pump (figure 2).

However, no notable biotic change, neither in traits such as size nor diversity, is observed in our open ocean region with the full return of the biological pump at approximately 1.8 Ma (line 2, figure 1a). The succession of acmes of nanofossil species in the Pacific [31] ends at this time (figure 2), yet, pre-extinction nanofossil size and ecogroups are not re-established until 3.5 Myr later, and diversity not until 10 Myr later.

Symbiosis is widespread in modern planktic foraminifera and allows populations to thrive in low-nutrient, oligotrophic environments [38]. The reacquisition of photosymbiosis [46] in planktic foraminifera did not lead to rapid diversification (figure 1d; electronic supplementary material, figure S2) [30,57]. We speculate that surface waters during the earliest recovery may have been rich in nutrients due to lower consumption, such that this ecology was not selected for. This speculation is supported by independent records of calcareous nanofossils which also do not begin to show a return to more oligotrophic taxa until 3.5 Myr later [31,37].

The contribution of the different size classes of foraminifera may give insight into the complexity of the food webs, as organisms tend to eat prey approximately a tenth of their size [58]. The equal contributions of the size classes present before the extinction suggest a complex food web. The dramatic shift to smaller shell sizes after the boundary suggests that larger organisms could not thrive [59,60], as food web complexity reduced, perhaps as mean food size



decreased and food chains shortened [20,61,62] an interpretation supported by a decline and long recovery in mid food chain predator fish, based on ichthyoliths (fossil fish teeth and shark dermal scales) (figure 2) [55].

In contrast with the recovery of the marine biological pump, plankton diversity and traits point to a much more drawn out return to pre-extinction states. Ecogroups recover around 4.3 Myr after the extinction, while size and diversity do not return to pre-extinction levels within the studied interval. Calcareous nanofossil diversity does not reach pre-extinction values for more than 10 Myr [34,63] and foraminiferal size even longer [35]. Similar long delays in diversity recovery are also documented for calcareous red algae (approx. 6 Myr to recover [64]), Neoselachian sharks (7 and 10 Myr [65]) and corroborated by other studies showing a macrofaunal genus level diversity lag of approximately 10 Myr [66,67].

The biological pump recovery (especially its strength) is likely driven by aspects of the marine community which do not fossilize, such as many microbes [68]. However, unexpectedly, larger size classes of organisms and specialists appear unnecessary for the recovery of the marine biological pump. Concurrently, the recovery of the biological pump does not result in a recovery of diversity and pre-extinction organism size [31]. The process of biotic recovery may be governed by other factors, such as niche creation, which are suggested to work on much longer time scales [36,67]. This interpretation supports the notion that rather than there being predefined 'niche' space (i.e. fixed ecological real estate) available to be filled or vacated at times of diversification or extinction, organisms themselves, and their interactions, 'construct' the environment they inhabit [69]. In this study, we speculate that increasing diversity created oligotrophic conditions, that in turn increased niche spaces which selected for novel traits such as symbiosis creating

feedbacks between environment (and the biological pump) and evolution.

## 5. Conclusion

The K/Pg extinction impacted the global biogeochemistry of the oceans and marine life for millions of years. Our data show that biotic recovery, as measured by trophic levels, microplankton size classes, and diversity of planktic foraminifera occurred much later than the re-establishment of a marine biological pump. Diversification of ecology in planktic foraminifers was linked to a return in the dominance of the surface symbiotic species adapted to lower nutrient conditions. These data suggest that a large range of nutrient conditions, including oligotrophic conditions, is necessary for high diversity independent of the marine biological pump recovery. Our findings highlight the need to link climate projections, models of primary production and ecology in both coastal and open ocean environments to improve our ability to project the repercussions of climate-induced extinctions or reorganization into novel environments on marine ecosystems and their services to people [70,71].

**Data accessibility.** Raw data used in this study can be found in the supplementary information file and Pangea.

**Competing interests.** We declare we have no competing interests.

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