A role for chance in marine recovery from the end-Cretaceous extinction

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Two contrasting ecological models have been proposed for the recovery from mass extinctions. The first posits that evolutionary recoveries are structured by trophic interactions alone, resulting in the predictable recovery of species richness and abundance earlier in lower trophic levels than in higher ones[1]. The second, the contingent model, holds that both chance and ecology are key to the structure of recoveries[2], thus precluding inherent predictability. Documented recovery patterns from the Cretaceous-Palaeogene mass extinction could support either model[1, 3-5], as most previous studies have lacked the high-resolution records of population abundance needed to discriminate them. Here we use high-resolution marine sediment records to reconstruct pelagic community structure during the Palaeogene recovery in three sites in the South Atlantic and North Pacific Ocean. We document heterogeneity in the timing of recovery between sites from the alternative community structure characteristic of early pelagic ecosystems. We show that the evolution of species richness and abundance is decoupled between two well-represented groups of phytoplankton and zooplankton, as well as between taxa within a single trophic level. Our results favour the contingent recovery model. Ecological and environmental mechanisms may account for any similarities in community structure among sites and for the eventual transition from early recovery to late recovery communities, while chance may explain intersite differences in the timing and path.

The recovery of open ocean ecosystems from the Cretaceous-Palaeogene (K-Pg) mass extinction provides a high-resolution record –spatially and temporally– of ecological reassembly following a massive disturbance of global scale. When viewed across different environments, post K-Pg community recovery patterns contain features of two contrasting theoretical models. The first of these, the trophic recovery model of Sole et al[1], postulates a sequential recovery of communities, with species richness and abundance increasing in lower trophic levels before higher ones. Implicit in the trophic model is the assumption that the ecological interactions leading to the evolutionary reassembling of communities will result in predictable recovery patterns[1]. Empirical support for this model, which aims to model recovery dynamics with the smallest set of ecological interaction possible, includes the synchronous recovery of $\delta^{13}C$ gradients, a proxy for organic flux from the surface ocean to the sea floor[6,7], and pelagic species richness, in two steps over the course of 3-4 million years following the K-Pg mass extinction[3,7,8] (Supplementary Fig. 1). In contrast, the freely evolving digital communities studied by Yedid et al.[2] illustrate the expectations of a contrasting theoretical model, which we call the contingent recovery model, in which individual digital communities are rebuilt with different speeds and directionality following the same perturbation. Yedid et al.'s results emphasize the importance of chance and history (e.g., contingency) in evolutionary reassemblies, with some communities acquiring full ecosystem functionality at low species richness[2]. Species and trophic interactions modulate recovery in both the trophic and contingent models[9], with the latter differing by allowing for unpredictable, or stochastic, processes. The contingent model gains empirical support from post-K-Pg terrestrial ecosystems which have decoupled recovery in plant diversity and insect feeding traces[5], and geographic variation in the timing of diversification and reassembly[4]. Here, we re-examine the fit of both models to empirical patterns of plankton assemblages to evaluate the degree to which oceanic recovery is a predicable versus a contingent process.

Our study focuses on the earliest interval of ecological recovery from the K-Pg mass extinction in a suite of Atlantic and Pacific Ocean drill sites (Supplementary Fig. 2). We refer to the plankton assemblages of this period as the "early recovery community" which we define on the basis of planktonic foraminiferal community composition, community-wide adaptations to unstable conditions, and the relative sedimentation of planktonic foraminifera (heterotrophic calcareous protists) to calcareous nannoplankton (algal primary producers; primarily coccolithophorids). We identify the early recovery on the basis of community structure rather than biogeochemical proxies[3,7] as we are chiefly interested in the recovery of pelagic ecosystems rather than biogeochemical cycling.

Early recovery community composition and structure is distinctly unlike that found before the extinction or during the later recovery. The early recovery community is defined in part by low diversity and production of calcareous nannoplankton[7,10] and the dominance of a typically rare group of planktonic foraminifera known as microperforate foraminifera[11] (Fig. 1b,c, 2b,c and Supplementary Fig. 3). The five microperforate genera that dominate early recovery communities[11-13] (*Guembelitria, Globoconusa*, *Parvularugoglobigerina*, *Woodringina*, and *Chiloguembelina,* Supplementary Fig. 4) evolved from the K-Pg boundary survivor *Guembelitria cretacea,* a late Cretaceous foraminifer that primarily inhabited productive coastal environments[12]. Early recovery foraminifera[11] and nannoplankton[10,14] are considered bloom or disaster taxa adapted to unstable environments. Similarly, the taxonomic composition of seafloor communities suggests marked variability in the flux of organic matter to the deep sea during this interval[15].

The early recovery community coincides with a large increase (2-8 fold) in the relative abundance of planktonic foraminifera to nannofossils (Figs. 1a, 2a, Supplementary Figs. 3, 5-10, calculations in Supplementary Methods). This increase in foraminiferal-sized fossils has been observed in five sites distributed globally[6,7,16] based on the relative weight of the coarse size fraction (>63μm or >38μm) and grainsize[17] (grain size patterns in Fig. 1a match a similar record from nearby Ocean Drilling Program Site 1212[17]). Previous work attributed the relative increase in foraminifera to improved carbonate preservation in the early Palaeogene rather than to a change in population abundance of foraminifera and/or nannoplankton[6]. However, three lines of evidence favour a change in abundance as the primary mechanism: i) higher % foraminifera in the early Palaeocene reflects the *decreased* sedimentation of dissolution-resistant nannoplankton counter to carbonate preservation expectation[18] (Fig. 1b, 2b, Supplementary Fig. 3), ii) the site with best carbonate preservation has the lowest flux of foraminifera (western Atlantic site, Fig. 3 and Supplementary Figs. 11-12), and iii) foraminifer shell weight –an independent proxy of carbonate preservation– is uncorrelated to changes in % foraminifera[19] (Supplementary Figs. 13-14). We conclude that the increase in % planktonic foraminifera must reflect a change in the abundance of living populations.

Thus, we infer that nannoplankton populations declined sharply across all sites, driving half to all of the observed increase in % planktonic foraminifera sized grains (Figs. 1b, 2b, and Supplementary Fig. 3). Foraminiferal abundances, in contrast, were markedly elevated in the eastern South Atlantic and North Pacific during the earliest recovery interval as compared to the later recovery (Fig. 3). This relative abundance peak in foraminifera occurs independently of a maximum in planktonic foraminiferal species richness (Supplementary Fig. 1) and counters the trophic recovery model (1) assumption that species richness is correlated to abundance and (2) prediction that lower trophic levels recover before higher parts of the food chain. Differences in the timing and directionality of recovery of abundance and species richness in and among taxa also challenge the non-ecological class of linear and logistic recovery models (as reviewed in Sole et al.[9]).

The trophic recovery model also assumes that recovery patterns are similar within a given trophic level, but this is not the case for early Palaeocene pelagic primary producers. Coccolithophorids, like planktonic foraminifera, suffered a mass extinction at the K-Pg boundary[10,20], followed by delayed recovery of abundance (Fig. 1b, Supplementary Fig. 1) and global species richness[8,10] (Supplementary Fig. 1). The magnitude of the loss and the relative time of the recovery of coccolithophorid diversity varied geographically[10], with delayed recovery in the North Pacific (310,000 years, Fig. 1d, low diversity coincident with "stressed" assemblage structure) versus a rapid rebound in the South Atlantic (e.g., "near immediate" as in Jiang et al.[10]; Fig. 2d).

Surprisingly, sites with the highest early recovery fluxes of organic matter from the surface to the deep ocean (as measured by Ba/Ti[21]) have depauperate (i.e., low richness, high dominance) coccolithophorid assemblages dominated by calcispheres and other opportunistic taxa[10,14] and delayed recovery. For example, our North Pacific site has simultaneously the most depauperate coccolithophorid assemblages globally[10] and Ba/Ti ratios that indicate the early recovery of organic matter to the sea floor equal to or exceeding those in the late Cretaceous[22] (Supplementary Figs. 15, 16). In contrast, sites in the Atlantic and Indian Ocean where Ba/Ti ratios fell by half or more[22] support relatively diverse, rapidly recovering coccolithophorid assemblages[10] (Fig. 2d and Supplementary Figs. 3, 17). Notably, other primary producers like diatoms and dinoflagellates suffered relatively mild K-Pg extinctions[20], with examples of primary producers recovering or exceeding pre-extinction abundance in the earliest Paleocene[23,24]. In addition, experiments have shown that modern coccolithophorids are outcompeted by other primary producers in unstable environments[25], like those that may have characterized the early recovery community interval. Delayed coccolithophorid recovery may simply reflect environmental instability or competitive exclusion in the early recovery community, rather than the general suppression of primary productivity.

Some communities in Yedid et al.'s digital experiments recover full functionality (in terms of the total expression of logic functions by trophic level) with alternative, low-diversity community structures[2]. Likewise, we find that early recovery communities are species poor, but in some cases support pre-extinction levels of export productivity. In the North Pacific, the absolute flux of planktonic foraminifera is 8-times greater in the early recovery community as compared to proceeding and subsequent time intervals (Fig. 1b, Supplementary Fig. 12), and accompanied by relatively stable organic fluxes (Ba/Ti ratios, Supplementary Fig. 15). In contrast, the absolute flux of early recovery foraminifera in the eastern and western South Atlantic was equivalent or less than the flux proceeding K-Pg boundary (Fig. 2b, Supplementary Fig. 3), although still greater than that found in later recovery communities. These two South Atlantic sites also display evidence of reductions in export productivity[15,22,26]. Thus, the success of the early recovery communities –as measured by the export of organic matter and the flux of foraminifera– varies among sites, with some as successful as pre-extinction or later recovery communities.

What then lead to the replacement of early recovery communities? One possibility is that early recovery community ecosystems were maintained by a particular environmental condition[27] such as unusually low export production[28]. However, our data show that export production varied substantially among sites. Environmental proxies also provide evidence against a trended environmental change leading to the termination of the early recovery community. For example, $\delta^{18}O$ values, a proxy of temperature and salinity, are similar before and after the demise of early recovery communities in the North Pacific, as is bulk sediment $\delta^{13}C$ (Supplementary Fig. 15,18).

In addition, the length of the early recovery differs substantially between sites, with durations of 200,000, 450,000, and 1,000,000 years in the eastern South Atlantic, North Pacific, and western South Atlantic, respectively (Fig. 1, 2 and Supplementary Figs. 3,5). A benthic foraminifer $\delta^{13}C$ event (Supplementary Fig. 15, from ~2.0 % to ~1.0%) coincides with the end of the early recovery in the North Pacific but not in the South Atlantic, suggesting diachroneity between the $\delta^{13}C$ shift (likely a global event) and the disappearance of the early recovery community. Hence, it seems unlikely that early recovery communities are simply responding to the global evolution of climate. Variable duration of the early recovery community compliments the recently described diachronous recovery of calcareous nannoplankton diversity[8,10]. It is notable that diachroneity of the early recovery does not appear to be an artefact of the method used to infer relative age (see Supplementary Methods and Supplementary Fig. 19), with support from multiple, independent age model estimates.

Alternatively, the transition from the early recovery communities to later communities may be enabled by a short-term environmental and/or ecological perturbation upsetting incumbent foodwebs. Early recovery pelagic assemblages are dominated by a sequential series of nannoplankton[14] and microperforate[11] species, with the dominant species differing across sites at a given time[11] (Fig 1c, 2c, Supplementary Fig. 3). Under this perturbation-turnover hypothesis, environmental or ecological perturbations allow changes in species dominance within early recovery communities and between early and later recovery communities. At present, there is some evidence for coincident environmental perturbations and assemblage turnovers in the North Pacific (Supplementary Fig. 15, microperforate turnovers coincide roughly with peaks in Ba/Ti), but comparable evidence for coincident perturbations and species turnovers is conspicuously lacking at other sites.

Here we find that alternative community structures can characterize recovering pelagic ecosystems for hundreds of thousands of years, with individual communities varying widely in their relative success (e.g., export productivity and standing population sizes). Ecology and trophic interactions may play a key role in structuring recoveries, but contingency and chance are likely to hinder predictive models of the timing and pattern of evolutionary recovery from global-scale disturbance.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Figure 1. Early ecological recovery in the North Pacific. Ecological recovery at ODP Site 1209, Shatsky Rise as revealed by (a) grain size distributions and % planktonic foraminiferal sized grains (white line), (b) the mass accumulation rate of planktonic foraminiferal (solid blue) and nannofossil (dashed green) sized grains, (c) planktonic foraminifera community composition, and (d) coccolithophorid faunal composition (colored bars), stress (black dotted line, non-metric multidimensional scaling axis 2 from Jiang et al.[10]), and species richness (grey dashed line). Coccolithophorid data collected at adjacent ODP Site 1210 by Bown[14]. Records figured with the Westerhold et al. age model[29] (K-Pg boundary at 65.28 Mya indicated across all panels in orange).

Figure 2. Early ecological recovery in the eastern South Atlantic. Ecological recovery at Walvis Ridge ODP Site 1262 (a,b,d; data in d from Jiang et al.[10] from ODP Site 1262) and DSDP Site 528 (c; data from D'Hondt and Keller[11]); see Figure 1 legend for panel details. Extensive Cretaceous sediment reworking indicated in (a) and coded by type of evidence for reworking. PF indicates planktonic foraminiferal evidence for reworking as noted in shipboard biostratigraphy (samples contain three common Cretaceous and no early Paleocene planktonic foraminifera[30]). N indicates nannoplankton evidence for reworking, with the youngest N marking the end of the exponential decline in highly abundant Cretaceous nannoplankton.

Figure 3. Cross-site comparison of calcareous and foraminiferal flux and % foraminiferal sized grains. (a) Calcareous flux, (b) foraminiferal flux, and (c) % foraminiferal sized grains at Shatsky Rise, North Pacific (ODP Site 1209; solid circles), Walvis Ridge, eastern South Atlantic (ODP Site 1262; asterisks), and Sao Paolo Plateau, western South Atlantic (DSDP Site 356, triangles).

Figure 1

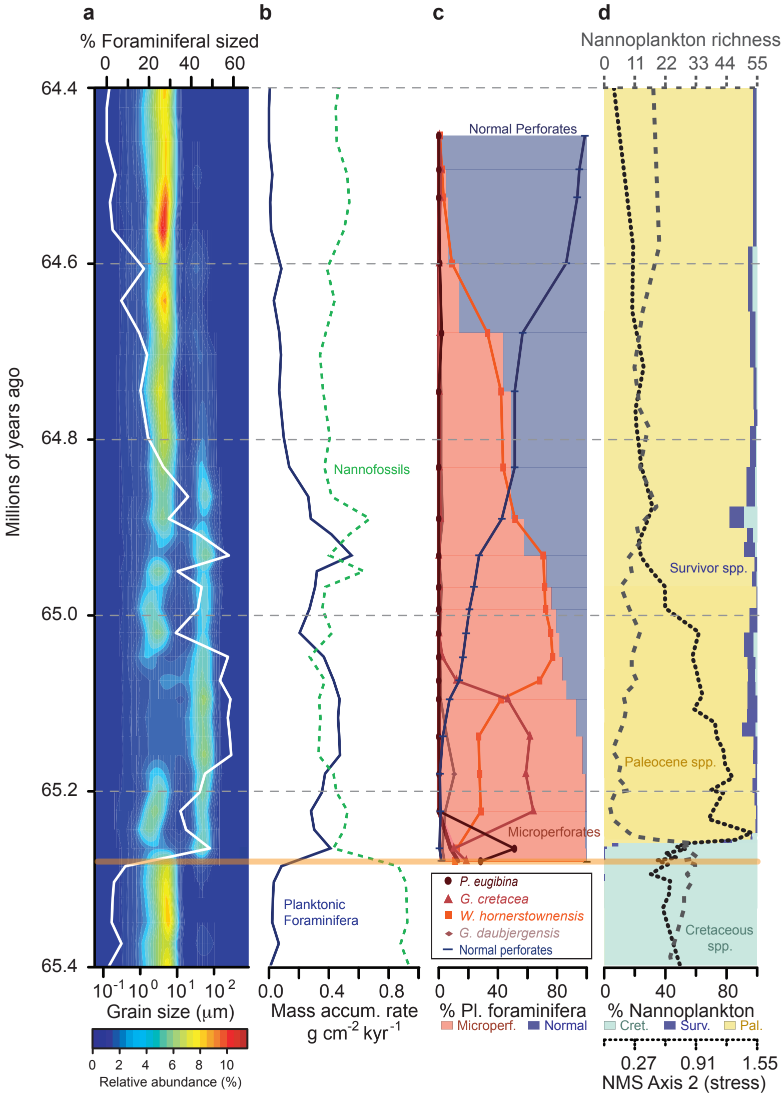

a
b
c
d
% Foraminiferal sized
0 20 40 60
Nannoplankton richness
0 11 22 33 44 55
Millions of years ago
64.4
64.6
64.8
65.0
65.2
65.4
Normal Perforates
Nannofossils
Survivor spp.
Paleocene spp.
Microperforates
Planktonic Foraminifera
Cretaceous spp.
P. eugibina
G. cretacea
W. hornerstownensis
G. daubjergensis
Normal perforates
10^{-1} 10^{0} 10^{1} 10^{2}
Grain size (μm)
0 2 4 6 8 10
Relative abundance (%)
0.0 0.4 0.8
Mass accum. rate
g cm^{-2} kyr^{-1}
0 40 80
% Pl. foraminifera
Microperf. Normal
0 40 80
% Nannoplankton
Cret. Surv. Pal.
0.27 0.91 1.55
NMS Axis 2 (stress)

Figure 2

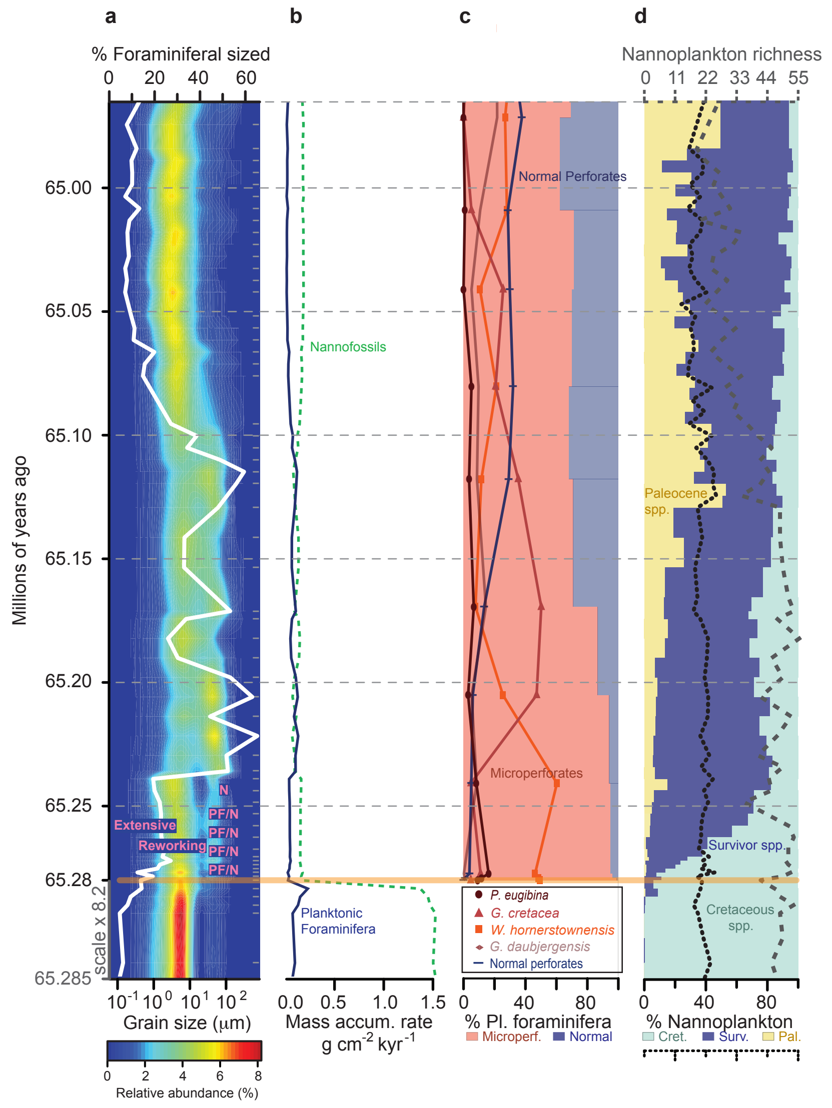
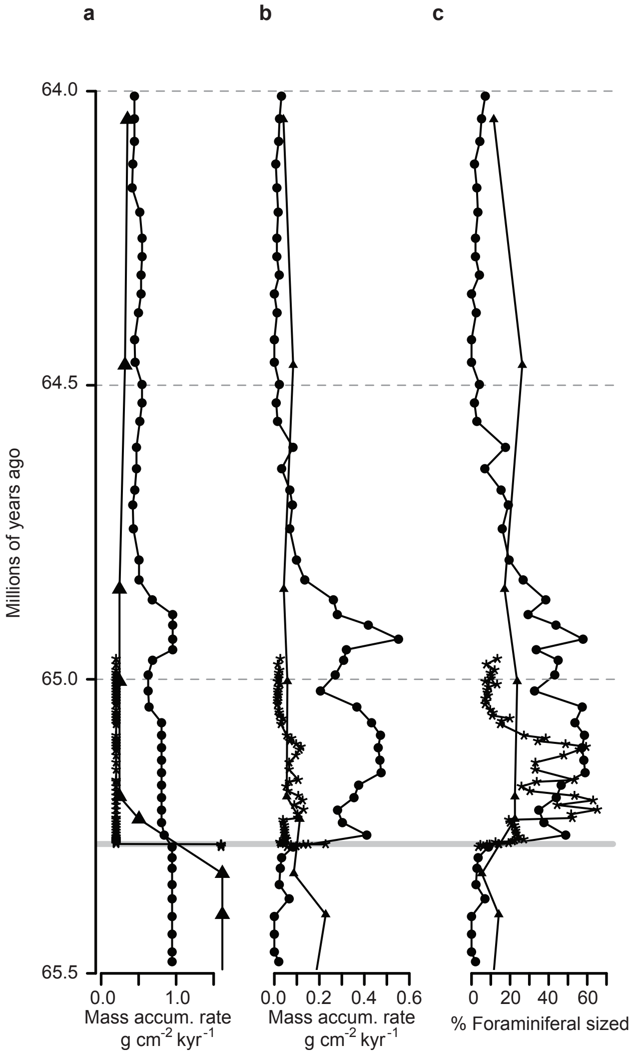

a
b
c
d
% Foraminiferal sized
0 20 40 60
Nannoplankton richness
0 11 22 33 44 55
Millions of years ago
65.00
65.05
65.10
65.15
65.20
65.25
65.28
65.285
scale x 8.2
N
PF/N
PF/N
PF/N
PF/N
Extensive
Reworking
10^{-1} 10^{0} 10^{1} 10^{2}
Grain size (μm)
0 2 4 6 8
Relative abundance (%)
Nannofossils
Planktonic Foraminifera
0.0 0.5 1.0 1.5
Mass accum. rate
g cm^{-2} kyr^{-1}
Normal Perforates
Microperforates
P. eugibina
G. cretacea
W. hornerstownensis
G. daubjergensis
Normal perforates
0 40 80
% Pl. foraminifera
Microperf. Normal
Paleocene spp.
Survivor spp.
Cretaceous spp.
0 40 80
% Nannoplankton
Cret. Surv. Pal.

Figure 3


a
b
c
64.0
64.5
65.0
65.5
Millions of years ago
0.0
1.0
Mass accum. rate
g cm-2 kyr-1
0.0
0.2
0.4
0.6
Mass accum. rate
g cm-2 kyr-1
0
20
40
60
% Foraminiferal sized