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Fungal contributions to ecological succession during the Cretaceous–Paleogene transition

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Abstract

Natural disasters, such as the end-Cretaceous meteorite impact that drove global ecosystem collapse and mass extinction, provide unique opportunities to study ecological recovery. Because elevated abundances of fungal spores relative to plant pollen and spores in the fossil record are widely interpreted to indicate ecological disruption, we examined sediments from a well-defined Cretaceous–Paleogene (K–Pg) boundary site in Colorado and identified three distinct fungal proliferative intervals. The earliest preceded the impact and coincided with intensified Deccan volcanism, implying that terrestrial ecosystems were already stressed before the bolide collision. High-resolution sampling, combined with comparisons of relative and absolute fungal abundance, revealed that the immediate post-boundary fungal interval developed through three sequential stages consistent with ecological succession. A later post-impact interval exhibited the highest relative and absolute fungal abundance and was dominated by small propagules, indicating a transition from decomposition to recovery by early colonizers. Some fossil spores resemble those of extant pathogenic fungi, raising the possibility that fungal pathogens imposed additional stress on surviving species. These findings suggest fungi played a more complex role in post-extinction recovery, serving not only as decomposers and potential pathogens, but also as mutualists facilitating the transition from fern-dominated landscapes to more complex Paleocene vegetation.

Introduction

Terrestrial ecosystems are complex networks of interacting organisms that coevolve toward dynamic equilibria with their habitats¹. Natural disasters disrupt this balance, causing widespread mortality while simultaneously altering the microbiomes associated with plants, animals, and soils². The microbial response to environmental disturbance, termed disaster microbiology^{3,4}, has far-reaching implications for ecosystem recovery, with both beneficial and detrimental consequences. Pyrophilous bacteria and fungi are among the earliest pioneer organisms to colonize barren substrates following disturbances such as wildfires^{5,6} and volcanic eruptions^{7,8}, where they facilitate ecosystem recovery through processes that include nutrient release and nitrogen fixation⁹. Environmental disruption can also enhance microbial dispersal and pathogenicity while simultaneously increasing host susceptibility to infection^{3,4}.

In the most extreme cases, natural disasters can occur on a global scale to trigger mass extinctions. Five such events have punctuated Earth's history¹⁰. The most severe of these, the end-Permian mass extinction approximately 252 million years ago, drove the extinction of an estimated 90% of marine species and 70% of terrestrial vertebrate species¹¹. An interval of widespread fungal proliferation has been documented in the aftermath of this catastrophe¹². Evidence for fungal proliferation associated with the most recent mass extinction at the end of the Cretaceous has likewise been reported from sites in both New Zealand¹³ and North America¹⁴, suggesting that this phenomenon may also have been a global occurrence.

The fungal kingdom, comprising approximately 155,000 formally described species from an estimated >3 million species¹⁵, plays vital, yet often underappreciated roles in terrestrial ecosystems¹⁶. Fungi are the principal decomposers of complex plant polymers such as cellulose and lignin¹⁷ and form essential mutualistic associations with plants, including the extensive global network of arbuscular mycorrhizal fungi, with an estimated biomass of approximately 300 megatons¹⁸. Because many fungi exhibit facultative lifestyle plasticity, they can shift between mutualistic, saprotrophic, and pathogenic lifestyles in response to environmental stress¹⁹. The end-Cretaceous mass extinction marked a pivotal transition in Earth's history, ending the nearly 200-million-year dominance of non-avian dinosaurs²⁰ and initiating the rise of mammals²¹. An intriguing possibility is that stress-induced shifts toward pathogenicity among the fungal taxa that proliferated during the end-Cretaceous extinction contributed to this transition, as non-avian dinosaurs may have been more susceptible than early mammals to fungal diseases, especially respiratory infections^{22,23}.

Although fungal spore morphology has evolved convergently across multiple lineages²⁴, complicating taxonomic assignment based solely on fossil spores, morphological characteristics such as spore size, shape, cellularity, and pigmentation nevertheless provide important clues to fungal ecology. Consequently, changes in fungal spore assemblages through time can yield valuable insights into the ecological succession of fungal communities during recovery from global catastrophes. Here, we analyze fossil fungal spore assemblages from the high-resolution strata in the Bowring Pit Cretaceous–Paleogene boundary site in Colorado spanning approximately 40 kyr before and after the Chicxulub impact. We identify three distinct intervals of fungal proliferation characterized by shifts in dominant spore morphotypes, spore size distributions, and abundance dynamics. Together, these data suggest a progression in fungal communities from a pre-impact stress phase during the Late Cretaceous, through a three-stage post-impact ecological succession that overlapped with the well-documented fern spike^{25,26}, to an early Paleogene phase when reestablishment of fungal–plant mutualisms may have facilitated ecosystem recovery.

Results

The Bowring Pit Late Cretaceous fungal interval

We previously reported a prolonged interval of fungal proliferation in the Denver Basin during the Late Cretaceous¹⁴, characterized by fungal spores comprising approximately 50% of the total assemblage of plant and fungal microfossils (Fig. 1a). The Bowring Pit, located in the West Bijou area of the Denver Basin in Colorado, is a well-studied K–Pg boundary site that features several hallmarks of the end-Cretaceous meteorite impact, including a distinct boundary clay layer, shocked quartz, an iridium anomaly, and a post-boundary fern spike^{25,26}. Uranium-lead dating of volcanic ash deposits interbedded throughout the section²⁷ provided temporal calibration that placed the Late Cretaceous fungal interval within approximately 30–10 kyr before the K–Pg mass extinction event.

The extended duration of this fungal bloom warranted re-examination at higher temporal resolution to identify any possible trends that may have occurred during the interval. Approximately 100 images of fossil fungal spores were acquired from each of ten sediment samples, spaced at roughly 2000-year intervals. Spores were classified into 18 morphotypes based on size, pigmentation, and cellularity (Fig. 1b, Table 1). Unicellate spores were the most common in the assemblage, accounting for 12 of the 18 morphotypes. Whereas the unicellate spores were relatively uniform in size and shape within each morphotype, there was considerable

variability among multicellate forms and as some did not appear intact, only their minimum size could be determined. Hence, the multicellate morphotypes are likely comprised of a diverse group of fungi that produced multicellate spores and have been grouped together into broad categories to simplify the analysis.

Comparison of morphotype abundances across the 10 samples (Fig. 1c) revealed that small, unicellate spores, represented by morphotypes 1-7, consistently dominated the assemblages, accounting for at least two-thirds of the fungal spores in every sample. Moreover, there was an observable trend towards increased relative abundance of the smallest spore morphotypes from the beginning to the end of the fungal bloom (Fig. 1c). To quantify this pattern, we measured the length of every unicellate spore from the 10 samples and calculated the mean and median spore size for each assemblage. Both metrics decreased in a statistically significant linear fashion over time (Fig. 1d), revealing a progressive reduction in spore size over the duration of the 20-kyr fungal interval.

Comparison of relative and absolute fungal abundance across the K–Pg boundary

Fungal proliferative events associated with the end-Permian and end-Cretaceous mass extinction events have been identified as intervals of elevated relative fungal abundance in palynological assemblages^{12–14}. Such fungal spikes are widely interpreted as evidence of increased fungal productivity, particularly given the availability of decaying organic matter in the aftermath of global environmental catastrophes. An alternative explanation, however, is that elevated relative fungal abundance in the palynological record simply reflects a severe reduction in plant productivity and abundance rather than an increase in fungal growth. To distinguish between these two possibilities, we derived estimates of absolute fungal spore abundances across the Bowring Pit K–Pg boundary section.

Total fungal spore counts within a defined volume of each sample were conducted in triplicate to estimate the abundance of fungal spores per gram of processed sediment. Although every effort was made to maximize fungal spore recovery¹⁴, these values represent recovered fungal spores per gram of sediment and therefore are likely to underestimate the true abundances owing to incomplete extraction and losses or breakage during sample processing. Moreover, these ancient assemblages may partly reflect a preservation bias toward melanized fungal morphotypes, as melanin confers exceptional resistance to degradation^{28,29}. Despite these limitations, our abundance estimates should accurately reflect differences within the section because all samples analyzed were lignites from the same lithological unit and were processed using the same protocol.

Absolute fungal abundances were similarly high during both the prolonged interval of fungal prevalence in the Late Cretaceous and the early Paleocene fungal bloom, reaching approximately 3×10^6 and 4×10^6 spores per g sediment, respectively (Fig. 2). In contrast, the K–Pg boundary fungal spike samples, K-36 and K-37, in which fungal spores comprised approximately 50% of the assemblage, exhibited among the lowest absolute abundances in the section, at only $\sim 1 \times 10^5$ spores per g (Fig. 2). Importantly, absolute fungal abundance increased by more than an order of magnitude in the two overlying samples, Pg-1 and Pg-2, reaching $\sim 1 \times 10^6$ and $\sim 3 \times 10^6$ spores per g, respectively (Fig. 2). This sharp increase in absolute fungal abundance coincided with the onset of the fern spike^{25,26}.

Post-impact fungal spikes in the Bowring Pit

We previously reported an interval of elevated relative fungal abundance in sediment samples in the early Paleogene, immediately above the K–Pg boundary¹⁴. However, our current analysis reveals that the absolute fungal abundance was initially low in the immediate aftermath of the impact (Fig. 2, 3a), presumably reflecting the devastation and extremely harsh environmental conditions associated with the calamity. Fungal abundance increased by approximately 10- to 30-fold during the subsequent ~ 1 kyr but because this increase coincided with the fern spike, fungal spores represented only a small proportion of the total palynological assemblages (Fig. 2, 3a). Approximately 10 kyr later, both relative and absolute fungal abundances increased even further, reaching approximately 75% of the total assemblage and about 4×10^6 spores per g sediment, respectively (Fig. 2, 3a). As fungal abundance changed dramatically across these four intervals, so too did the dominant spore morphotypes within each assemblage.

The initial increase in relative fungal abundance immediately above the boundary (K–Pg-1) represented by samples K-36 and K-37, consisted of a relatively diverse assemblage of fungal spores, dominated by dark brown, ellipsoidal spores approximately 20 μm wide and 35 μm long (Fig. 3b, Table 1), which comprised approximately one-third of the fungal spore assemblage¹⁴. The two cells each possessed an apical pore and were separated by a single transverse septum that was positioned centrally in most specimens but was occasionally displaced asymmetrically. Scanning electron microscopy revealed smooth, thick spore walls lacking ornamentation (Fig 3b). Morphologically, these spores resemble the form genus *Dyadosporites*, first identified in Late Cretaceous sediments from Colorado³⁰. The remaining two-thirds of the fungal assemblage in this interval, described previously¹⁴, ranged from small unicellate amero-spores to large multicellate phragmo-spores. K–Pg-1 was also distinguished by an unusually high abundance of hyphal

fragments, which comprised approximately 30% of total fungal microfossils¹⁴ compared with only ~10% in the other fungal spikes identified in the Bowring Pit section.

Because the overlying samples, Pg-1 and Pg-2 contained only 20-30% fungal spores relative to the total assemblage, they were not examined in detail in our previous study. However, their substantially higher absolute fungal abundances relative to K-Pg-1 suggest that they represent a continuation of the post-impact fungal interval, which we designate K-Pg-2 and K-Pg-3. To characterize changes in morphotype composition, approximately 100 fungal spores from each sample were imaged and measured. This analysis revealed a transition from the large, multicellate spores characteristic of K-Pg-1 to smaller, predominantly unicellate spores in K-Pg-2 and K-Pg-3, which was accompanied by a reduction in overall spore diversity. K-Pg-2 consisted of approximately 35% lightly pigmented, unicellate ellipsoidal spores that averaged ~15 μm in length (Fig. 3c, Table 1). These were occasionally observed as attached pairs, suggesting that the bipolar structures may represent hilar attachment scars rather than germ pores. This morphotype was also present in K-Pg-1 and K-Pg-3 but was less abundant, comprising only ~14% and ~4% of the fungal spore assemblages, respectively. An additional 31% of fungal spores in K-Pg-2 consisted of heavily pigmented, unicellate globose spores averaging ~10 μm in diameter (Fig. 3c, Table 1). This morphotype remained dominant in K-Pg-3, where it accounted for 46% of the assemblage, together with heavily pigmented, unicellate lacrymoid spores averaging ~10 μm in length, which comprised a further 44% (Fig. 3d, Table 1).

The fungal spike that occurred approximately 10 kyr after the K-Pg boundary during the early Paleocene similarly exhibited low spore diversity and closely resembled the latter stages of the post-impact fungal succession. The assemblage was dominated by heavily pigmented, unicellate globose spores approximately 10 μm in diameter (46%) and heavily pigmented, unicellate lacrymoid spores (44%) (Fig. 3e, Table 1). The latter were somewhat larger than those observed in K-Pg-3, averaging ~13 μm in length. The remaining ~10% of the assemblage in the Pg spike, described previously¹⁴, consisted of thin-walled, unicellate ellipsoidal spores exhibiting taphonomic deformation.

Size and cellularity trends in Bowring Pit fungal intervals

For the five intervals spanning the K-Pg boundary, we quantified the proportions of small (≤ 10 μm), medium (10-20 μm), and large (> 20 μm) spores (Fig. 4a) as well as the proportions of unicellate, dicellate, and multicellate forms (Fig. 4b). The Late Cretaceous fungal bloom (K) was dominated by unicellate spores (83%) and most spores fell within the small (48%) and medium (42%) size classes (Fig. 4). The first boundary interval (K-Pg-1) was the only assemblage

dominated by large spores (63%), many of which were dicellate or multicellate (Fig. 4). Both spore size and cellularity changed markedly across the three boundary intervals, with assemblages showing a progressive shift toward higher proportions of small, unicellate spores (Fig. 4). The fungal spike in the early Paleogene (Pg) was composed almost entirely of unicellate spores that were predominantly small to medium in size (Fig. 4).

Discussion

Periods of fungal proliferation following global ecological catastrophes have been documented after both the Permian–Triassic¹² and K–Pg mass extinctions^{13,14}. However, our current analysis of the Bowring Pit K–Pg boundary section revealed a more complex pattern of fungal dynamics than the single post-impact bloom of saprotrophic decomposers typically envisioned. Instead, we identified three distinct proliferative intervals, a finding that may reflect improved recovery of fungal spores by our preparation protocol, which avoided the strong acids and fine sieving commonly used in standard palynological processing³¹. Comparisons of relative and absolute spore abundances together with changes in morphotype assemblages across these sequential intervals suggest a progression from a pre-impact stress phase, through a three-stage, post-impact ecological succession, to an early Paleogene ecosystem recovery phase (Fig. 5).

Both relative and absolute fungal fossil spore abundances were elevated during an approximately 20-kyr interval of the Late Cretaceous. This interval coincided with the Poladpur phase of the Deccan Traps eruptions³² and an approximately 5°C cooling episode recorded in the Denver Basin³³, suggesting that prolonged environmental stress could have destabilized terrestrial ecosystems and favored the proliferation of opportunistic fungi in disturbed habitats. Comparison of relative and absolute fungal spore abundances in sediments above the K–Pg boundary reveals a three-stage ecological succession during the first ~1.5 kyr following the Chicxulub impact. The initial stage was characterized by high relative fungal abundance but low absolute abundance, indicating that fungal dominance primarily reflected the collapse of terrestrial plant communities rather than a substantial increase in fungal productivity in the devastated post-impact landscape. During the second stage, absolute fungal abundance increased by approximately an order of magnitude whereas relative abundance declined as pioneer vegetation, particularly ferns^{25,26}, rapidly colonized barren substrates. Fungal abundance nearly tripled again during the third stage, but fungal spore proportions remained comparatively low because fern proliferation continued to dominate the recovering ecosystem. As ecological recovery progressed

and vegetation transitioned from fern-dominated communities toward more established forests, a final fungal proliferation characterized by both high relative and high absolute abundance occurred approximately 10 kyr after the boundary. Unlike the immediate post-impact fungal spike that was likely dominated by saprotrophic decomposers, this later proliferative interval is consistent with the re-establishment of fungal-plant interactions, including endophytic and mycorrhizal associations, that facilitated ecosystem recovery and forest development.

Although nearest living relative (NLR) approaches have been applied recently to dispersed fossil fungal spores for paleoenvironmental reconstruction³⁴, most of the spores in our assemblages were small propagules lacking diagnostic features such as septation or ornamentation. Given the extensive morphological convergence among distantly related lineages³⁵, we could not confidently assign these fossils to extant genera or species. Moreover, because only a small fraction of the estimated > 3 million extant fungal species have been formally described, these ancient fossils, if they have modern counterparts, may belong to the vast group of undescribed fungal lineages collectively referred to as 'dark fungi'¹⁵. Instead, we considered each assemblage as a whole and used morphological characteristics such as size, shape, cellularity, and pigmentation to infer the ecological strategies of the fungi that produced them. The pre-impact proliferative interval was dominated by small, globose spores and exhibited a significant decrease in mean spore size over the approximately 20-kyr interval. Because smaller spores are generally dispersed more efficiently than larger spores³⁶, this trend is consistent with selection for an r-strategist lifestyle³⁷ that maximizes reproductive output and dispersal while minimizing investment in individual propagules under unstable environmental conditions, such as those associated with intense Deccan Traps volcanism. In contrast, the immediate post-impact interval (K–Pg-1) assemblage was dominated by relatively large dicellate and multicellate spores, together with abundant hyphal fragments, suggesting fungal communities adapted for saprotrophic growth on abundant necromass generated by the mass extinction rather than for rapid dispersal and colonization. During the subsequent post-impact stages and continuing into the early Paleogene interval, dominant morphologies shifted once again toward small, simple spores. The accompanying shift from predominantly elongated to globose spores is consistent with a transition from a saprotroph-dominated assemblage toward fungal communities increasingly characterized by endophytic and mycorrhizal lifestyles²⁴. Indeed, re-establishment of fungal-plant interactions essential for nutrient acquisition would be a critical early step in the recovery of terrestrial forests.

Overall, the assemblages are broadly consistent with melanized conidia produced by several extant lineages of Ascomycota, particularly Dothideomycetes³⁸, although these

similarities should not be interpreted as taxonomic assignments. Modern members of this group, such as *Alternaria*³⁹ and *Curvularia*⁴⁰, include species that are saprotrophs, mutualists, and opportunistic pathogens of both plants and animals. If broad morphological similarities to extant species also reflect comparable ecological strategies, including facultative pathogenicity, fungal proliferation during the K–Pg transition may have imposed additional biological stress on organisms already challenged by widespread environmental disruption. Although infectious diseases are rarely considered in reconstructions of past mass extinction events because they seldom leave traces in the fossil record, pathogens have undoubtedly imposed considerable selective pressure throughout evolutionary history. The early Paleogene fungal interval is not currently associated with any known catastrophic geological event but because it exhibited both the highest relative and absolute spore abundances, may have represented the greatest potential danger for fungal diseases as large inocula can substantially increase the pathogenic potential of otherwise weakly virulent microorganisms⁴¹. Moreover, this fungal bloom was dominated by small, simple spores, some of which fall within the size range capable of alveolar and lower airway deposition^{42,43}. If these fungi included opportunistic pathogens, respiratory infection may have posed a greater risk to any surviving non-avian dinosaurs owing to anatomical differences between the avian-style respiratory system of non-avian dinosaurs and mammalian lungs²³.

In addition to fungal spores, we observed fragments of fungal hyphae in our assemblages, and these were particularly abundant in the immediate post-impact strata. Since none of these hyphal fragments displayed evidence of the clamp-connection structures characteristic of basidiomycetes hyphae, the fungal assemblages were likely dominated by ascomycete fungi. Indeed, *Ascomycota* is more highly represented than *Basidiomycota* in the fossil record³⁵, which may partly result from taphonomic preservation bias toward more persistent ascospores. Furthermore, as ascomycetes are generally more thermotolerant than basidiomycetes⁴⁴, the ascomycetes predominance could also reflect the much hotter climate of the Late Cretaceous, with global mean surface temperatures in the range of 6–14°C higher than pre-industrial levels⁴⁵.

Pigmentation was a defining feature of the fossil fungal spores in our assemblages, with most spores exhibiting heavy melanization. Melanin imparts structural rigidity and resistance to oxidation and soil acids, thereby enhancing spore persistence over millions of years. Indeed, overrepresentation of melanized fungal spores in the fossil record is a well-appreciated instance of taphonomic bias²⁹. Hence, our assemblages of preserved spores may not be fully representative of all the fungal species that proliferated during the K–Pg transition. Nevertheless, among the spores that persisted, we observed distinct shifts in dominant morphotypes across sequential intervals. Because the lithology and preparation methods were consistent among these

intervals, the observed changes likely reflect fungal community responses to environmental stresses and ecological succession, even though our assemblages may represent incomplete subsets of these ancient communities.

In summary, detailed analysis of fossil fungal spore assemblages from sediments spanning the K–Pg transition revealed three successive proliferative intervals that differed markedly in abundance, morphology, and inferred ecological function. We interpret these changes as evidence that fungal communities responded dynamically to environmental disturbance, serving not merely as passive bystanders of the global catastrophe, but as active participants in terrestrial ecosystem succession and recovery. Future investigations of additional high-resolution K–Pg boundary sections in other locales are warranted to determine if the patterns of fungal succession described at the Colorado site represent a global response to the end-Cretaceous mass extinction. We extended our analysis of fungal proliferative events to include not only relative abundance estimates, but also absolute abundance measurements, which ranged between 1–4 million spores per gram of sediment in the K–Pg boundary strata. These estimates probably underestimate true abundances because of incomplete recovery as well as preservation bias of heavily melanized spores, revealing that fungi were remarkably abundant in ecosystems before and after the K–Pg extinction event and that the Earth was essentially a fungal world, at least in the Denver Basin of ancient Colorado.

Methods

Palynological processing

Our method for non-acid based extraction was described in detail previously¹⁴. Briefly, 2 g of sediment was crushed using a mortar and pestle, heated for 1 h at 60°C in a 3% Alcojet solution, then allowed to soak overnight at room temperature. Samples were then treated with 1:2 w/w sodium hexametaphosphate for 40 min at 60°C while stirring, sieved through a 500 µm filter, then concentrated by centrifugation in a saturated solution of sodium metatungstate. Following several washes with distilled water, strew mount slides were prepared from unstained or Safranin-stained samples, embedded using 4% polyvinyl alcohol, and mounted using Eukitt Quick-hardening mounting medium.

Light and scanning electron microscopy

Light microscopy was performed on an Olympus AX70 microscope under bright field illumination. Images were captured using QCapture-Pro 6.0 software with a Retiga 1300 digital charge-coupled device camera. Positions of imaged microfossils on strew mount slides were recorded using an England Finder (EF) and are provided in Table 1.

Fungal spore sizes were measured in pixels from 40× photomicrographs using ImageJ software and the conversion factor 0.0167 µm/pixel was applied to determine sizes in micrometers. Fungal spore relative abundances were calculated for each sample as the percentage of fungal microfossils out of total counts of approximately 100-500 fungal and plant microfossils. Absolute abundance estimates were made by performing total fungal spore counts in triplicate from diluted samples and then multiplying by the dilution factor to calculate the number of spores in the original sample. Total counts for the three replicates ranged from approximately 80-270. For each absolute abundance measurement, mean and standard deviation, reflecting the technical error of the three replicate counts, was determined using GraphPad Prism software.

For scanning electron microscopy, samples were fixed in 2.5% glutaraldehyde, 3 mM MgCl₂, in 0.1 M sodium cacodylate buffer, pH 7.2 overnight at 4°C. After buffer rinse, samples were postfixed in 1% osmium tetroxide in 0.1 M sodium cacodylate buffer for 1 h on ice in the dark. Following a distilled water rinse, samples were dehydrated in a graded series of ethanol and left to dry overnight in a desiccator with hexamethyldisilazane (HMDS). Samples were mounted on carbon coated stubs and imaged at 3 kV on a JEOL SEM (JSM-IT700HR) at the Material Characterization and Processing Center of the Johns Hopkins University Whiting School of Engineering.

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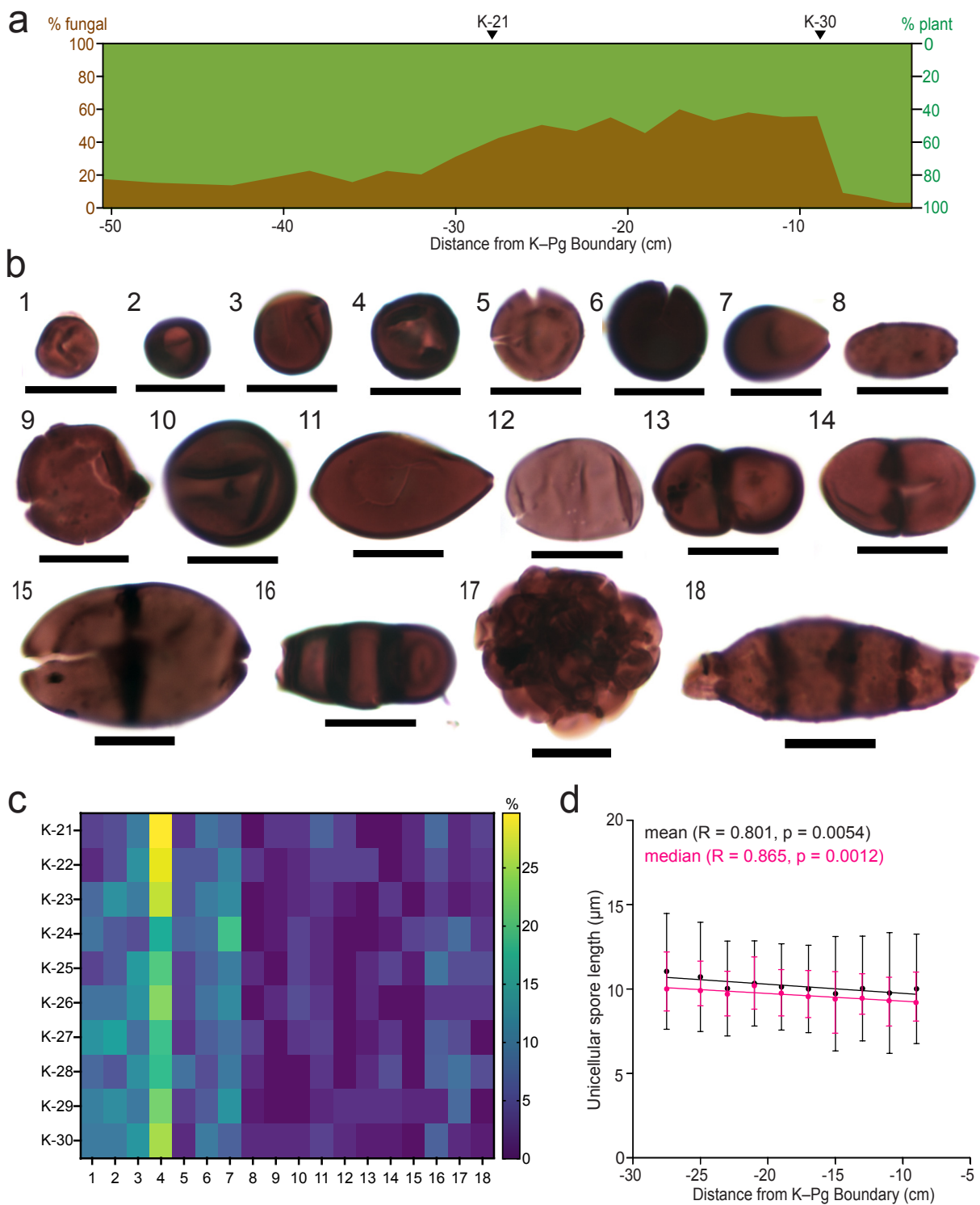


Fig. 1. Fungal spore morphotypes in the Bowring Pit Late Cretaceous spike. (a) Plot of relative proportions of fungal (brown) and plant (green) microfossils in sediment samples spanning 50 cm below the K–Pg boundary. Relative to the low ~20% background level, fungal spores were proportionally more abundant at approximately 50% of the total assemblage in 10 samples (K-21 to K-30). (b) Representative photomicrographs of the 18 spore morphotypes identified in the Late Cretaceous fungal interval (scale bar = 10 μm). Morphotype descriptions, slide name, and EF coordinates for each image are provided in Table 1. (c) Heat map of the percentage of each of the 18 fungal spore morphotypes in the 10 fungal bloom samples. (d) Linear plots of mean (black) and median (pink) unicellular fungal spore size in each sample reveal a decrease in spore size from the beginning to the end of the fungal bloom.

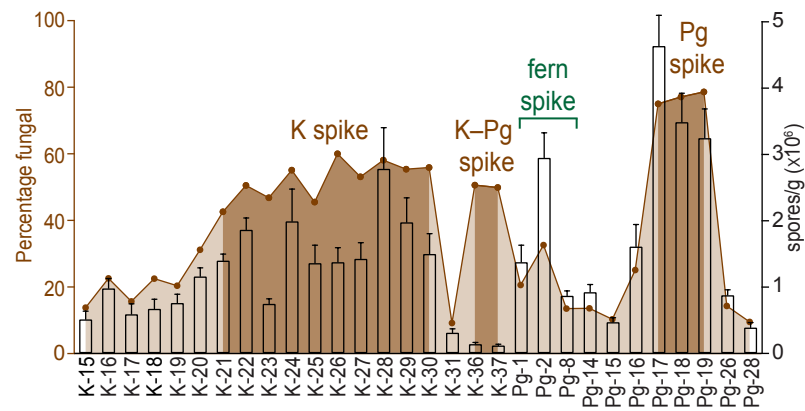


Fig. 2. Overlay of relative and absolute fungal abundance in the Bowring Pit K–Pg boundary section. Line graph of relative abundance data (brown), reported previously¹⁴ with positions of three spikes indicated by darker shading. Bar graph of estimated absolute abundance (black) shows concordance with relative abundance for the K and Pg spikes but a delayed spike in abundance after the K–Pg boundary that coincides with the previously documented fern spike^{25,26}.

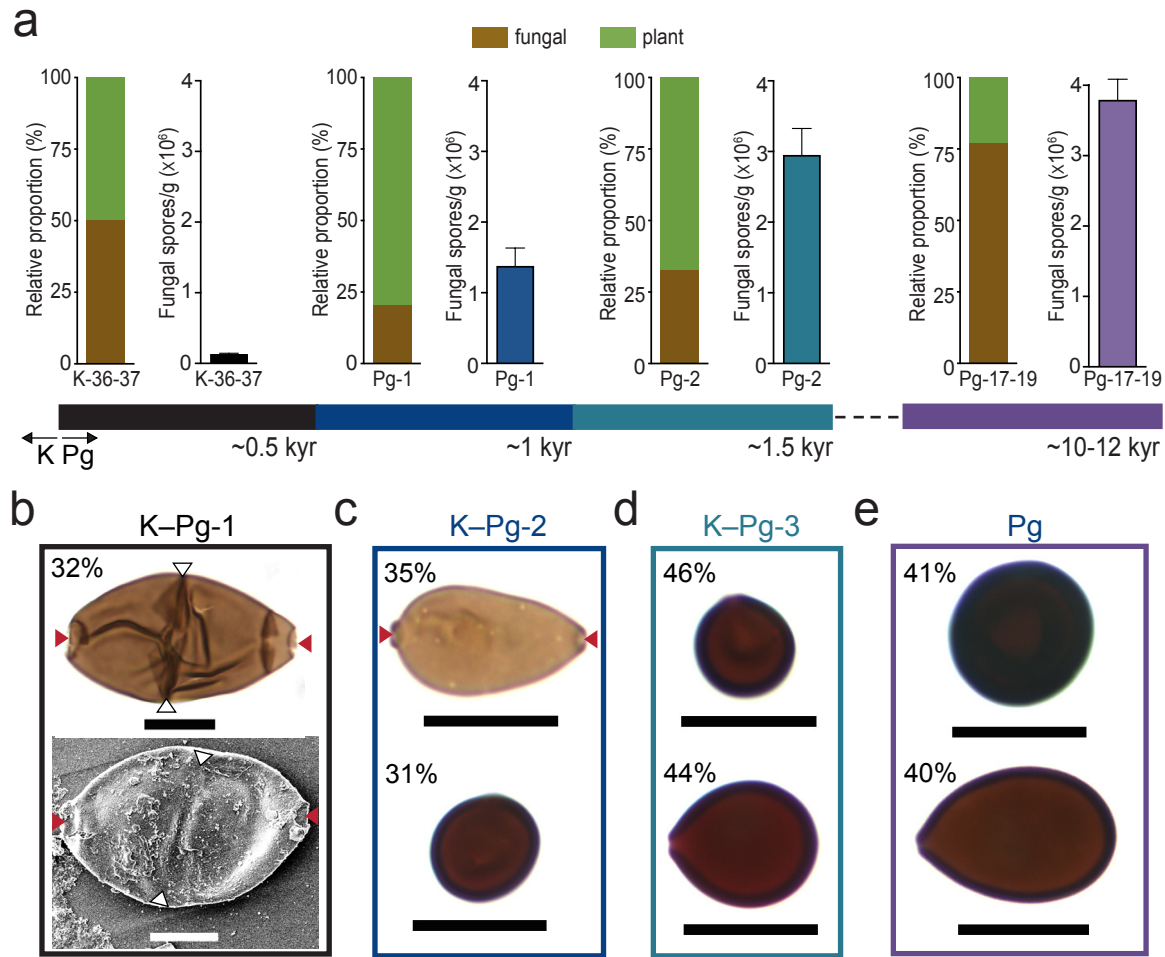


Fig. 3. Bowring Pit post-boundary fungal intervals. (a) Bar graphs of relative (left) and absolute (right) fungal abundance in four intervals above the K–Pg boundary with time estimates relative to the boundary provided below. Absolute abundance measurements are reported as mean and standard deviation of three replicate counts. (b) Representative photomicrograph (upper) and scanning electron micrograph (lower) of the dominant spore morphotype in the first post-boundary interval, K–Pg-1. Apical pores (red arrows) and transverse septum (white arrows) in the large, dicellate ellipsoidal spores are indicated. (c–e) Representative photomicrographs of the most abundant spore morphotypes in K–Pg-2, K–Pg-3, and Pg intervals, with percentages indicated. The most abundant spore in K–Pg-2 (c, upper) was a lightly pigmented, unicellate ellipsoidal spore with polar hilar attachment scars (red arrows). Also abundant in K–Pg-2 were small, heavily pigmented, unicellate globose spores (c, lower). The most abundant spore morphotypes in K–Pg-3 (d) and Pg (e) were small, heavily pigmented, unicellate spores that were globose (upper) or lacrymoid (lower). Morphotype descriptions, slide name, and EF coordinates for each image are provided in Table 1. Scale bar = 10 μ m.

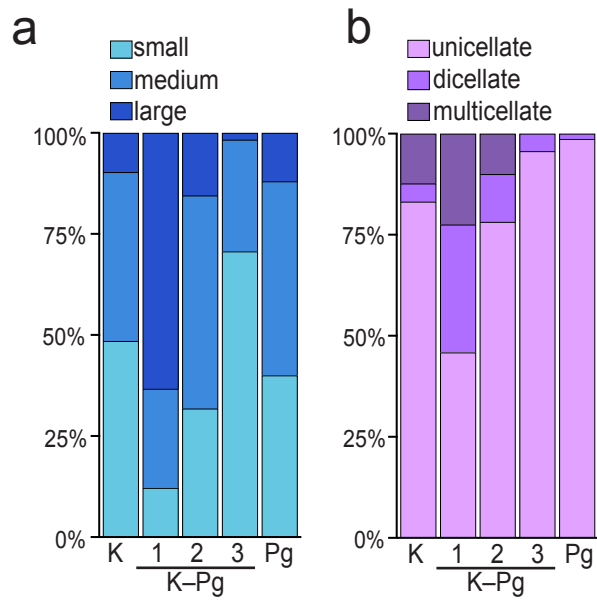


Fig. 4. Comparison of size and cellularity distributions across the K–Pg boundary. Graphs of (a) relative proportions of small ($\leq 10 \mu\text{m}$), medium ($10\text{--}20 \mu\text{m}$), and large ($> 20 \mu\text{m}$) spores and (b) relative proportions of unicellate, dicellate and multicellate spores in fungal spikes during the Late Cretaceous (K), post-boundary (K–Pg-1, -2 and -3) and early Paleogene (Pg).

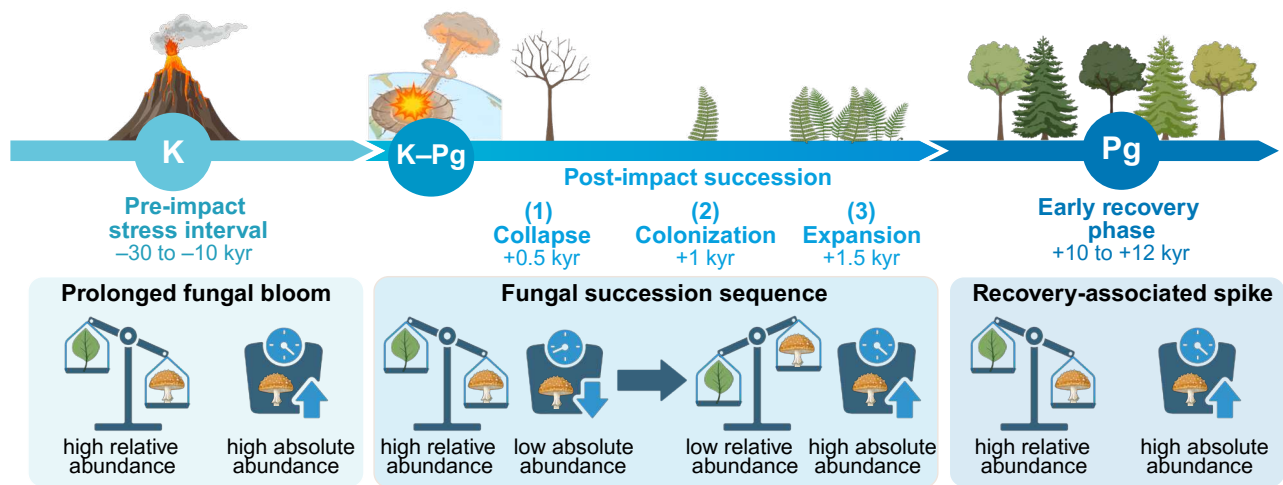


Fig. 5. Model of ecological and fungal succession across the K–Pg boundary. A prolonged fungal bloom occurred during the Late Cretaceous (K), a three-phase fungal succession followed immediately after the bolide impact (K–Pg) and a fungal spike associated with ecosystem recovery occurred during the early Paleogene (Pg). Image was created using BioRender.com.

Table 1. Fungal spore morphotypes in representative images from Figures 1 and 3.

Interval	Morphotype Description	Slide name	EF location ¹
K	1) unicellate globose, < 8 µm, light to medium pigmentation	040626_BP-K-30_2A	P371
K	2) unicellate globose, < 8 µm, heavy pigmentation	040626_BP-K-25_2A	T484
K	3) unicellate globose, 8.1-10.5 µm, light to medium pigmentation	031726_BP-K-28_1B	D170
K	4) unicellate globose, 8.1-10.5 µm, heavy pigmentation	040626_BP-K-27_2A	M394
K	5) unicellate globose, 10.6-13 µm, light to medium pigmentation	031726_BP-K-27-1B	G164
K	6) unicellate globose, 10.6-13 µm, heavy pigmentation	040626_BP-K-23_3A	G440
K	7) unicellate lacrymoid, 8-16 µm, medium to heavy pigmentation	031826_BP-K-24_1A	N482
K	8) unicellate ellipsoid, 11-16 µm, light to medium pigmentation	040626_BP-K-30_2B	S150
K	9) unicellate globose, >13 µm, medium pigmentation	031726_BP-K-30_1A	Q150
K	10) unicellate globose, >13 µm, heavy pigmentation	040626_BP-K-26_2A	Q450
K	11) unicellate fusiform, 11-23 µm, medium to heavy pigmentation	040626_BP-K-30_2B	L190
K	12) unicellate ellipsoid, 13-33 µm, light to medium pigmentation	031826_BP-K-21-1B	S191
K	13) dicellate globose, 14-25 µm heavy pigmentation	040626_BP-K-22_2A	O420
K	14) dicellate ellipsoid, 14-24 µm, light-medium pigmentation	040626_BP-K-29_2A	G480
K	15) dicellate ellipsoid, 27-44 µm, light to medium pigmentation	031826_BP-K-21_1A	N490
K	16) multicellate elongate, 12-28 µm, light to medium pigmentation	031726_BP-K-28_1B	N220
K	17) multicellate cluster, 11-37 µm, medium pigmentation	040626_BP-K-26_2A	F431
K	18) multicellate elongate, 30-82 µm, medium to heavy pigmentation	040626_BP-K-23_3A	U420
K–Pg-1	dicellate ellipsoid, diporate, 20-44 µm, medium pigmentation	022626_BP-K-36_1B	P150
K–Pg-2	1) unicellate ellipsoid, 9-20 µm, light pigmentation	062526_BP-Pg-1_1A	Q410
K–Pg-2	2) unicellate globose, 8-15 µm, heavy pigmentation	082625_BP-Pg-1-1A	Q460
K–Pg-3	1) unicellate globose, 7-13 µm, heavy pigmentation	082625_BP-Pg-2-1A	L421
K–Pg-3	2) unicellate lacrymoid, 6-11 µm, heavy pigmentation	082625_BP-Pg-2-1A	L473
Pg	1) unicellate globose, 5-14 µm, heavy pigmentation	052626_BP-Pg-18_1A	J454
Pg	2) unicellate lacrymoid, 9-20 µm, heavy pigmentation	052626_BP-Pg-17_1A	P430

¹Reference position of each fungal fossil recorded using an England Finder (EF) slide.