

1 **Long term resilience decline in plant ecosystems across the Danian Dan-C2**  
2 **hyperthermal event, Boltysch crater, Ukraine.**

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9 **critical transition**

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**ABSTRACT**

12 Mass balance calculations indicate that a massive amount of  $\delta^{13}\text{C}$ -depleted carbon was  
13 released into the early Danian atmosphere in volumes comparable with the younger  
14 Paleocene-Eocene thermal maximum (PETM). This Danian hyperthermal event (the Dan-  
15 C2) has been documented from the fill of the Boltysch meteorite crater, Ukraine. Palynofloras  
16 recovered from the Boltysch crater fill show a trend from mesic forest to savannah ecosystem  
17 dominance on a millennial scale across the hyperthermal inception with no abrupt  
18 compositional shift. This longer term trend is overprinted by moisture availability oscillations  
19 reflecting orbital forcing. Forcing is not directly tracked by the oscillations, which are  
20 composed of mesic forest and savannah palynofloras separated by rapid critical transitions.  
21 The absence of an ecological collapse at the Dan-C2 indicates that plant ecosystems  
22 experienced dominant forcing from orbital cyclicity, rather than a stochastic temperature rise.

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## INTRODUCTION

25 While gradual climate change dominates the long term geological record, short periods of  
26 rapid global warming on a deca-millennial scale (19k.y. Cui et al., 2010; 30k.y. Murphy et al.,  
27 2011), followed by slower recovery over tens to hundreds of thousands of years, have  
28 become the subject of intensive study. These hyperthermal events are commonly  
29 documented by pronounced negative carbon isotope excursions (CIE) caused by the  
30 addition of thousands of petagrams of  $^{12}\text{C}$ -enriched carbon to the ocean-atmosphere system  
31 and thus record major short-term perturbations of the global carbon cycle. The Paleogene  
32 period includes several of these hyperthermal events, the Dan-C2 event at ca. 65.2 Ma  
33 (Quillévéré et al., 2008), the Latest Danian event at ca. 61.7 Ma (Westerhold et al., 2008;  
34 Bornemann et al., 2009), and the Danian-Selandian transition event at ca. 61 Ma (Speijer,  
35 2003). However, the best documented hyperthermal remains the Paleocene-Eocene  
36 Thermal Maximum (PETM, see review by McInerney & Wing, 2011). The earliest of the  
37 Paleogene hyperthermals, the Dan-C2 event, has been documented in marine carbonate  
38  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  records from the Atlantic (Quillévéré et al., 2008; Westerhold et al., 2011),  
39 western Tethys (Coccioni et al., 2010) and from the fill of the Boltysh meteorite crater,  
40 Ukraine (Gilmour et al. 2013, 2014). The marine Dan-C2 sections are well constrained by  
41 magnetostratigraphy and micropaleontology, being interpreted as post-dating the K/Pg  
42 boundary by less than 300 k.y. (Quillévéré et al., 2008).

43 Although the rate of climate change during these hyperthermal events is regarded as being  
44 an order of magnitude less than current anthropogenic climatic warming (Ridgwell &  
45 Schmidt, 2010; Haywood et al., 2011), paleontological records from these hyperthermals  
46 elucidate ecosystem responses to high levels of atmospheric  $\text{CO}_2$ . The majority of  
47 investigations of hyperthermal events have been conducted on marine sedimentary  
48 sequences, since they are more commonly preserved and held to be complete (e.g. Zachos  
49 et al., 2005). These examples document rapid environmental change at event initiation, often  
50 associated with biotic turnover and extinction of benthic organisms (Thomas, 1998; 2007).  
51 Studies of the terrestrial record of hyperthermal events are less common and apparently of

52 lower resolution than their marine counterparts (e.g. Hesselbo & Peinkowski, 2011; Wing &  
53 Currano, 2013). Accordingly, the rate of terrestrial environmental and ecosystem change,  
54 and its consequences are less well understood.

55 Plant macrofossil records across the PETM CIE demonstrate changes in floral dominance  
56 and diversity. Macrofloras from central North America show an incoming of dry subtropical  
57 taxa (Smith et al, 2007), with relatively rapid floral shifts across the hyperthermal inception  
58 (Wing et al., 2009). The PETM palynofloral record from this region is reported to lack clear  
59 indications of rapid compositional change, although these records are more detailed than  
60 those from other hyperthermal intervals (e.g. Riding et al., 2013). This paucity of data adds  
61 importance to the high resolution non-marine record of the Dan-C2 hyperthermal event in the  
62 fill of the Boltysh meteorite crater, Ukraine (Gilmour et al., 2013 and Figure 1). Mass balance  
63 calculations of a ~3‰ negative bulk organic  $\delta^{13}\text{C}$  excursion (Gilmour et al., 2014), indicate  
64 that a massive amount of  $^{12}\text{C}$ -enriched carbon was released into the early Danian  
65 atmosphere in volumes comparable with the PETM. In addition to the similarity of the Dan-  
66 C2 to the PETM, it has a carbon-isotope record comparable to the geometry recorded at  
67 the Toarcian hyperthermal event (Kemp et al., 2005; Figure 2).

68 Because the Boltysh crater formed on the Proterozoic basement of the Ukrainian shield  
69 immediately prior to the K/Pg event (Kelley & Gurov 2002; Jolley et al., 2010), steady state,  
70 lacustrine conditions endured through the post-impact early Danian. Palynofloras derived  
71 from these lacustrine sediments show a series of compositional and diversity changes  
72 across the hyperthermal (Gilmour et al., 2013; 2014), but apparently lack any abrupt  
73 modification in composition at the CIE inception. Here, we examine the apparent disconnect  
74 between the palynological record of vegetation community change and the evidence for a  
75 geologically rapid period of climate warming.

## 76 **Ecological Analysis**

77 Palynofloral data derived from the analysis of 418 sediment samples at ~1m spacings taken  
78 from borehole 42/11 (Gilmour et al., 2013) were subjected to diversity and dominance

79 analysis and to ordination techniques to elucidate ecological trends. Detrended  
80 correspondence analysis was undertaken to identify major environmental trends within the  
81 palynofloras (using MVSP, Kovach, 2002 and PAST 3, Hammer et al., 2001). First, data  
82 reduction was undertaken to reduce 'noise', involving the removal of taxa which formed <2%  
83 of the total palynoflora. The reduced data set was then smoothed by transformation to  
84 square roots. A scatter plot of the first two DCA axes (27.8% cumulative variation) was used  
85 to identify taxa with similar spatial distributions (Figure 3). In contrast, the whole of the data  
86 set was utilised for indirect data analyses, results being smoothed using either Loess  
87 averaging or Box-Cox transformation (Hammer et al., 2001).

88 The botanical composition and stratigraphical distribution of the normalised palynofloral  
89 botanical affinity groups was calibrated to DCA sample axes (Figure 4), and utilised to define  
90 biomes. In the absence of previously defined earliest Paleocene biomes, these were  
91 constrained by taxonomic composition to Maastrichtian biomes (Figure 1 and Willis &  
92 McElwain, 2002). These are in turn derived from plant macrofossil data and are closely  
93 related to the palynofloristic provinces of Herngreen et al (1996).

#### 94 **Vegetation response to hyperthermal inception**

95 Analysis of frequency distribution changes in botanical affinity groups (Figure 4)  
96 demonstrated that there was no abrupt compositional change at the CIE inception, isotope  
97 stage 2 (Gilmour et al., 2013). Instead, overall increased dominance of Normapolles and  
98 Juglandaceae from isotope stage 1 to the mid point of stage 2 was matched by a  
99 corresponding overall decline in mesic humid taxa (Pinaceae, Cupressaceae,  
100 Polypodiaceae, Cyathaceae, Fagaceae). These data indicate an extended period of plant  
101 community adaptation to warmer temperatures and decreased moisture availability.  
102 However, this long term trend is overprinted by shorter frequency compositional oscillations.  
103 Previously identified in the post K/Pg boundary - isotope stage 1 interval as moisture  
104 availability oscillations (MAO), these oscillations continue into the CIE and recovery stage  
105 (Jolley et al., 2013). MAO's are recorded by shifts from Pinaceae, Cyathaceae,

106 Polypodiaceae and Cupressaceae dominance, to late oscillation Normapolles, Juglandaceae  
107 and Platanaceae dominance over stratal thicknesses of 20-25m. These geologically rapid  
108 changes are interpreted by reference to botanical affinities, as representing shifts from warm  
109 temperate humid forest to a winterwet, or savannah-type open vegetation ecosystem. Over  
110 the period from the K/Pg boundary to mid isotope stage 2, there was a shift to increased  
111 moisture stress in the wet phase of each oscillation as a consequence of continued longer  
112 term warming. Evident as a decrease in frequency and diversity of humid temperate taxa  
113 (Figure 5), this trend is apparent in the Temperate:Winterwet ratio and from falling taxonomic  
114 distinctness. This last factor documents decreasing diversity of palynofloras at generic and  
115 family level, a response to increased stress from lower moisture availability. The  
116 consequence of the long term warming and drying climate and the overprinted MAO's, was a  
117 succession of local palynofloral extirpation (i.e. extinctions in the Boltys record) events  
118 (Figure 5). These events are noticeable in the dryer, later phases of MAO's 2-6 (Figure 5)  
119 and mark the sequential extirpation of mesic taxa in response to increasing aridity.

120 Milankovitch-scale cyclicity in paleopalynological data has been reported from sediments as  
121 old as the early Mesozoic (e.g. Bonis et al., 2010). The Boltys MAO oscillations are  
122 interpreted here as likely reflecting either 21ky (precession) or 41ky (obliquity) cycles (Jolley  
123 et al., 2013). Oscillations show an offset correlation (Figure 5) to cyclicity within the bulk  $\delta^{13}\text{C}$   
124 data, which have been in turn related to precession or obliquity cycles (Gilmour et al., 2013).  
125 Taken together with the relatively high paleolatitude of the Boltys crater (~49°N, Figure 1),  
126 the wet phase – dry phase moisture fluctuation is compatible with variation in insolation over  
127 41k.y. obliquity cycles.

## 128 **Discussion**

### 129 **No Catastrophic Regime Change at the CIE**

130 The palynological data derived from the 42/11 core samples shows that there was no  
131 catastrophic change in the plant ecosystem at the Dan-C2 CIE inception. A trend towards  
132 increased dominance of the winterwet biome palynofloras is recorded from the post K/Pg

133 boundary to within the Dan-C2 CIE, best reflected by the increased dominance of the  
134 Normapolles group. Despite this long term trend, there is change in plant ecosystem  
135 composition at the CIE inception, but it does not differ significantly from compositional shifts  
136 in the post K/Pg to Dan-C2 CIE interval. It is possible to derive two initial interpretations of  
137 the gradual response recorded in the palynological data across the Boltysch Dan-C2 CIE; that  
138 the early Danian hyperthermal had a gradual, rather than rapid onset, or that botanical  
139 factors control the large scale vegetation response to rapid climate change. Rapid  
140 temperature change  $>10^{\circ}\text{C}$  over 20 k.y. ( $\sim 5^{\circ}\text{C}$  MAT, Wing & Currano, 2013) has been  
141 recorded at the inception of the PETM (Murphy et al., 2010), with these temperatures  
142 persisting for a further 80 k.y. – 113 k.y. (Murphy et al., 2010; McInerney & Wing, 2012).  
143 Comparable change is interpreted from the correlative  $\delta^{18}\text{O}$  early Danian Dan-C2 event  
144 (Quillevère et al., 2008). These records negate any gradual warming hypothesis, although  
145 the magnitude and nature of the events remains a subject for debate (Sluijs & Dickens,  
146 2012).

147 Because the Boltysch palynofloral record does not exhibit a critical ecosystem transition in  
148 response to rapid climate change at Dan-C2 inception, compositional shifts in the palynoflora  
149 have been investigated in detail. It is informative to compare the Boltysch record of long term  
150 change with the chronostratigraphy of the better documented PETM. A duration of 20 k.y.-  
151 30 k.y. for the Boltysch CIE onset and a subsequent 80 k.y. – 113 k.y. of persistent high  
152 temperatures (Figures 4, 5), would predict temperature declines from within MAO7  
153 (assuming a  $\sim 41$  k.y. MAO duration). Botanical composition (Figure 4), kurtosis and  
154 taxonomic distinctness (Figure 5), provide evidence of a warm-dry maximum during MAO7 –  
155 MAO8 at the peak  $\delta^{13}\text{C}$  excursion. These oscillations are reflected in the lithology and  
156 wireline logs, intervals with lower moisture availability floras corresponding to outbuilding of  
157 lake-margin turbidite fans (Figure 5). This correlation likely reflects increased erosion in the  
158 catchment from mesic forest breakdown and its replacement by lower biomass, open  
159 savannah. This transition is comparable to responses to forest breakdown recorded in the  
160 Holocene of the Mediterranean (Sadori et al., 2011). Shifts between warm temperate and

161 winterwet biomes in the interval from the K/Pg boundary to within the lower part of the CIE  
162 indicate millennial vegetation community response to short-term forcing. In contrast, rapid  
163 warming at the CIE (isotope Stage 2) inception contributed to a buffered vegetation  
164 community response over 10's k.y.

165 What factors could have overridden rapid land surface temperature warming at the CIE,  
166 resulting in its uncoupling from vegetation community change? Part of the answer appears to  
167 lie in the position of the Boltysh impact crater in relation to biome boundaries (Figure 1).  
168 Vegetation records from other hyperthermals, in particular their palynofloras, show variability  
169 in frequency of pre-excursion taxa, but few inceptions or extirpations (Harrington &  
170 Jaramillio, 2007). The long term post K/Pg boundary to mid isotope stage 2 decline in humid  
171 temperate Cupressaceae and Pteridophyta (Figure 4) reflects a transition from warm  
172 temperate to winterwet biomes over ~300 k.y., marking the northward shift of the biome  
173 boundary. One potential reason for the uncoupling of rapidly increasing temperature from  
174 vegetation biome change is therefore inherent in the sensitivity of the site relative to the  
175 biome boundary. Putative locations to the north of present day Ukraine could record  
176 vegetation change wholly within the warm temperate biome.

### 177 **Pre-adaptation**

178 Similar records of repeated variation in temperature/moisture availability and  $\delta^{13}\text{C}$  have been  
179 recorded as an interval of isotopic variation in the Toarcian hyperthermal (Hesselbo and  
180 Pienkowski, 2011), and in some PETM records (e.g. North Sea, Kender et al., 2012). In the  
181 Boltysh record, repeated switches between dominantly humid temperate and dominantly  
182 winterwet vegetation reflect ~160 k.y. of temperature and moisture availability fluctuation  
183 from the K/Pg boundary to within the CIE. Alternation between stable biome states would be  
184 expected to result in enhanced physiological adaptation within species and within floral  
185 communities. Repeated resurgences of humid temperate taxa leading up to the winterwet  
186 biome maxima supports an interpretation of preadaptation to moisture stress in regional  
187 vegetation dynamics. Reservoirs of physiologically adapted species and pre-adapted

188 communities could have existed in local enclaves around the island archipelago (see Daly &  
189 Jolley, 2015) site of Boltysch. However, a migrational connection to central Europe cannot be  
190 eliminated. Comparisons by the authors of the Boltysch palynofloras with other southern  
191 European Danian – Selandian palynofloral records failed to identify clear evidence for  
192 endemism (e.g. Kedves & Russel, 1982). Re-invasion of plants from potentially upland  
193 refugia into an open savannah-type ecosystem could have been relatively rapid. Significant  
194 Mediterranean Quaternary migrational lags occurred over 100's years (Ammann et al.,  
195 2013); in the k.y. context of the currently sampled Boltysch palynofloral record these would  
196 appear instantaneous. Within the Boltysch palynoflora, repeated minor extirpation events are  
197 recorded, particularly during the warm, dry phases of MAO2 and MAO4-MAO6 (Figure 5).  
198 This repeated elimination of sensitive warm temperate taxa would have resulted in  
199 increasing Normapolles dominance. As a consequence, palynofloras recovered from MAO7  
200 - MAO8 represent the period of optimum community adaptation to the winterwet regime.

#### 201 **Alternative states**

202 The lack of significant changes in the palynological records of PETM sites in Wyoming and  
203 Alabama have previously been attributed to floral inertia (Wing et al., 2003, 2009). While  
204 this may have contributed to vegetation conservatism during early Danian humid climate  
205 phases in the Boltysch record, it would have been of lesser significance in the lower biomass  
206 winterwet vegetation community (Bailey, 2014). In contrast to inertia, the Boltysch record  
207 shows repeated, rapid alternations between parallel stable biomes in the interval prior to and  
208 during the Dan C2 CIE (Figure 5). Intuitively, an extrinsically forced event such as Dan-C2,  
209 would have instigated a critical transition from mesic temperate forest into a winterwet stable  
210 state (Scheffer et al., 2001; Veraart et al., 2012; van Nes & Scheffer 2007). Such a critical  
211 transition is not observed in the Boltysch data, which shows the continuation of MAO's, albeit  
212 at decreasing amplitude (Figure 5). Post K/Pg boundary Milankovitch-mediated oscillations  
213 in vegetation ecosystem composition could be expected to track multi-dimensional climate  
214 forcing. Simple tracking of climatic warming from cool/wet to warm/dry orbital-forced cycles  
215 would have yielded a sinusoidal response in mesic and savannah-type vegetation



216 communities. This is not the response observed in the Boltysch record. Both mesic forest and  
217 savannah biomes appear stable during respective cool and wet, to warm and dry phases of  
218 each MAO, reflecting resilience within each biome to orbitally-forced climate change (see  
219 examples in Scheffer et al, 2001). Transition between these stable mesic forest and  
220 savannah states was rapid, being completed within ~8% of the total 20m-25m MAO strata  
221 thickness (a transition duration of approximately 3 k.y. assuming 41 k.y.obliquity cycles).

222 Because of the rapidity of the transitions between mesic and winterwet biomes, and their  
223 repetition at declining amplitude, they can be compared to 'flickering' responses in present  
224 day biological populations or systems, prior to regime shifts (Dakos et al, 2013, 2015).  
225 However, the current Boltysch record displays this putative flickering over 10's k.y.s, an order  
226 of magnitude greater than flickering of Dansgaard – Oeschger events in the last glacial  
227 period (Dakos et al., 2013), and significantly longer than the years duration of other  
228 Holocene records (e.g. Wang et al., 2012). Because of this long duration event frequency,  
229 the rapid shifts between mesic and winterwet biomes are interpreted here as being  
230 comparable to critical transitions leading to regime (biome) shifts. Their pattern of biome  
231 stability followed by rapid transition to an alternative stable state (biome) follows patterns  
232 modelled from slow environmental change towards a tipping point (Dakos et al, 2015). In the  
233 Boltysch ecosystem the tipping point marks the time at which winterwet or mesic forest biome  
234 resilience was overcome by climate forcing. Following this interpretation, flickering would be  
235 expected occur in plant ecosystems prior to these critical transitions in late mesic forest and  
236 winterwet biome states. However, the shorter time frequency of such flickering is not reliably  
237 observed in the current Boltysch data set, remaining below the resolution of 1m spaced  
238 samples.

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### Conclusions

240 From the palynological evidence recovered from a sequence of 1m spaced samples in  
241 Boltysch borehole 42/11, it is clear that vegetation response to rapid climate change at the  
242 CIE inception was long duration transformation, not regime change of ecosystems. The long

243 term trend demonstrates the overall decrease in moisture availability prior to, and  
244 subsequent to the CIE inception. This is superimposed onto a record of shorter duration  
245 shifts between stable warm mesic forest and winterwet biome dominance. Repeated critical  
246 transitions between these mesic and winterwet plant biome states occurred in the pre-CIE  
247 and CIE intervals. Repeated rapid switching of organisms, or ecosystems between stable  
248 states has been termed flickering in comparative modern ecological systems (Wang et al.,  
249 2012). Although the Boltysht record could be viewed as demonstrating long periodicity  
250 flickering prior to the Dan-C2 hyperthermal event, this is not supported by the absence of  
251 regime change at the CIE. Stronger candidates for critical shifts are recorded at the  
252 boundaries between stable biomes, occurring between MAO's at winterwet – mesic forest  
253 biome shift and within MAO's at mesic forest – winterwet shift. The duration and repetition of  
254 these MAO's indicates that they record plant ecosystem responses to orbital forcing. The  
255 presence of stable ecosystems separated by critical transitions indicates that plant  
256 community pre-adaptation of mesic species played a significant role in building mesic forest  
257 resilience. Contributory factors in this pre-adaptation would have been repeated migrations,  
258 floral inertia within mesic forests and individual taxon ecological tolerances which could  
259 have overlapped between temperate and winterwet biome states.

260 The magnitude of shifts between biome states became suppressed after the CIE inception,  
261 reflecting greater resilience in the winterwet biome with increased temperature/low moisture  
262 following the CIE inception. The Boltysht record indicates that Milankovitch-mediated cyclicity  
263 (likely obliquity) operated stronger forcing on plant ecosystems than the Dan-C2  
264 hyperthermal. Particular to the Boltysht record may be the coincidence of the cooler, high  
265 moisture availability (mesic forest) phase of MAO5 with the rapid increase in temperature  
266 implied by the negative CIE inception. Such superposition could have mitigated rapid  
267 warming, lessening the effect on regional vegetation. However, this would potentially be  
268 succeeded by amplification of the continuing  $\delta^{13}\text{C}$ -depleted carbon excursion in the later,  
269 warmer and dryer phase of MAO5. This response is not evident.

270 The current analysis of the Boltysh palynofloral record has highlighted areas of  
271 uncertainty which invites future investigation. Firstly, it is desirable to examine other  
272 hyperthermal records for pre-CIE (isotope stage 1 and earlier) variability in the  $\delta^{13}\text{C}$   
273 record. In several terrestrial hyperthermal records, sampling of the interval prior to  
274 the hyperthermal is absent or sporadic, preventing comparison. It is therefore  
275 possible that vegetation community and climate instability in the period between the  
276 K/Pg and CIE inception may be a consequence of post K/Pg ecosystem instability.  
277 Until the pre-CIE interval of other hyperthermal is investigated in detail it is not  
278 possible to differentiate between instability inherent in the approach to a  
279 hyperthermal, or perturbation following the K/Pg event.

280 From the Boltysh record, it is evident that vegetation change does not simply mirror  
281 potential forcing from either orbital cyclicity or stochastic global temperature change.  
282 This observation is practical because of the high deposition rate, steady state  
283 depositional system of the Boltysh crater. It emphasises how conceptions of rapid  
284 change in climate proxies in the geological record are likely distorted by the fidelity of  
285 individual rock records and the physical limitations of sampling.

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433 Figure 1. Location map of the Boltys impact crater, showing the extent of Maastrichtian  
434 biomes in the northern hemisphere (after Willis & McElwain, 2002).

435 Figure 2. Comparison of bulk  $\delta^{13}\text{C}$  from three hyperthermal events. The complete record  
436 for each individual CIE was scaled proportionally, giving a common alignment of the  
437 inception and termination of the individual CIE's. There is evident similarity between the  
438 Toarcian CIE, Yorkshire, UK (Kemp et al., 2005) and the early Danian Boltys record  
439 (Gilmour et al., 2013). A less clear comparison is made to the PETM at Polecat Bench,  
440 Wyoming (Wing et al., 2005). This terrestrial record may differ because of the greater  
441 sample spacing. In contrast, the marine PETM record of ODP 1263 (Murphy et al., 2010)  
442 displays a smoothed trend comparable to that seen in both the Toarcian and Danian events.

443 Figure 3. Plot of first two axes of detrended correspondence analysis of the Boltys  
444 palynofloras recovered from 42/11. Many of the taxa which comprise the warmest  
445 communities belong to the extinct polyphyletic Normapolles group which lack a detailed  
446 knowledge of their botanical affinity (Daly & Jolley, 2015). Botanical affinities of the taxa  
447 indicate that Axis 1 reflects temperature/biome, while axis 2 reflects moisture availability.

448 Figure 4. Stratigraphical plot of the frequency of taxa recorded in the Boltys 42/11 borehole.  
449 The taxa are shown as percentages of the whole pollen/spore flora. The first two axes from  
450 the DCA analysis of the same data set are plotted; Axis 1 reflects biome or temperature, axis  
451 2 reflects moisture availability. Heavy dashed horizontal lines are used for major biome  
452 changes which are identified with reference to the DCA axes and the taxa frequency plots.  
453 Light dashed lines identify events of lesser significance. Dashed line 'a' marks the transition  
454 from warm temperate to winterwet, coinciding with the CIE inception. Light dashed line 'b'  
455 marks the winterwet biome maximum. Light dashed line 'c' marks a significant change in the  
456 crater hydrological system, and is coincident with the re-appearance of abundant  
457 *Botryococcus braunii* (Chlorophyceae; see Gilmour et al., 2014). Dashed line 'd' marks the  
458 onset of warm temperate biome which shows a transition into a cool temperate biome at line  
459 'e'. All data is plotted alongside the bulk  $\delta^{13}\text{C}$  record (Gilmour et al., 2013).

460 Figure 5. Lithological and statistical record of the 42/11 borehole, showing wireline logs and  
461 indirect indicators derived from palynology data. The GR (gamma ray log) and GGR (gamma  
462 – gamma logs) show natural gamma radiation and formation density. Note the appearance  
463 of reworked ejecta below 560m as high GR log values. The build-out of crater margin fans  
464 during the winterwet phase of MAO3 and the decline in grain size of clastic material during  
465 the main CIE is also evident from the GR log. The warm temperate – winterwet ratio plot is  
466 labelled to show MAO's 1-11, compositional change in the biomes above this requiring  
467 different ratio plots for the late-recovery and post-recovery periods. It is noteworthy that  
468 following the Dan-C2 CIE inception, the frequency of MAO's remains constant, but the  
469 amplitude decreases (Standard deviation of temperate:winterwet 571m- 486m, 4.98; 360m-  
470 485m, 0.34). This reflects the overall dominance of the winterwet biome following the CIE.  
471 All other indirect indicators derived from the palynological data are plotted as smoothed lines  
472 (S) using Loess average smoothing to highlight longer term trends. Diversity in the pollen  
473 and spore palynoflora is measured by Menhinick's richness index which calculated  
474 the ratio of the number of taxa to the square root of sample size. Along with  
475 Brillouin's diversity index these are used to reduce bias introduced by lithological  
476 variation, and closely follow Species Richness. Evenness compares the actual, to  
477 the maximum possible diversities. Floras with the greatest evenness occur during  
478 the CIE, with subsequent decrease and wide fluctuations in the recovery interval  
479 where single taxa can dominate assemblages. In contrast the emphasis placed on  
480 the single taxon records, Distinctness (Taxonomic Distinctness, Clarke & Warwick,  
481 1999) utilises the taxonomic hierarchical relationship of the palynofloral components.  
482 This index highlights the possibility that recovery from the maxima of the CIE, which  
483 begins within Stage 2 (see Brillouin's Index and Kurtosis) is not paralleled by a  
484 taxonomic recovery into Stages 3 and 4. . All data is plotted alongside the bulk  $\delta^{13}\text{C}$   
485 record and the cyclicity present in these data (Gilmour et al., 2013, 2014).