

1 **Centennial to decadal vegetation community changes linked to orbital and solar**
2 **forcing during the Dan-C2 hyperthermal event.**

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13 **Abstract**

14 Formed close to the K/Pg boundary, the Boltsh meteorite crater, Ukraine, preserves
15 >400m of lacustrine sedimentary rocks which include a record of the early Danian Dan-C2
16 hyperthermal event. Abundant pollen, spores and algae recovered from these sediments
17 have yielded a cyclic record of plant ecology change paced by ~21 ky orbital precession
18 cycles. New, higher resolution sampling across the inception of the Dan-C2 hyperthermal
19 event has identified oscillations in vegetation community ecology at sub-orbital periods of
20 ~2 ky, ~200 y, and ~11 y. These are consistent with possible Hallstatt, DeVreis/Suess, and
21 Schwabe solar cycles, respectively. Rapid regime shift from savanna to a mesic forest
22 ecosystems was paced by ~21 ky precession, with the shift likely occurring in <200y. Prior to
23 regime shift, ~2 ky (i.e. possible Hallstatt) oscillations between mesic- and winterwet-
24 dominated plant communities increased in intensity, suggestive of ecological flickering.

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28 *Supplementary material (detrended correspondence, and changepoint analysis, palynological*
29 *frequency data for DCA groups and core photographs) is available at*

30

31 **Introduction**

32 Hyperthermal events represent some of the most extreme changes in Earth's surface
33 conditions of the past 200 Ma, and are associated with transient increases in global
34 temperatures (typically $\sim 5^{\circ}\text{C}$), changes in $p\text{CO}_2$, changes in hydrology, mass extinction, and
35 ocean acidification and deoxygenation (e.g. Zeebe & Zachos, 2013). Hyperthermals such as
36 the PETM (~ 56 Ma), early Toarcian (~ 182 Ma) and early Aptian (~ 120 Ma) have been
37 considered to be Earth system analogues for anthropogenic warming scenarios, because
38 there is evidence that warming during these events was associated with the transfer of large
39 amounts ($>10^3$ petagrams) of carbon to the oceans and atmosphere (Kemp et al., 2005;
40 Mehay et al., 2009; Kirtland Turner & Ridgwell, 2013; Alexander et al., 2015; Zeebe et al.,
41 2014). Despite the utility of studying these events, uncertainties in age models and the
42 limited resolution of the geological record has hindered the comparison of these deep time
43 events with anthropogenic climate change. This uncertainty has been compounded by recent
44 suggestions that warming occurred at rates orders of magnitude slower than anthropogenic
45 forced change (Zeebe et al., 2016).

46 An essential part of elucidating the nature of hyperthermals and evaluating their impact on
47 life on Earth is the acquisition and study of complete, high fidelity records. Notably, there is
48 a general lack of non-marine records of ancient hyperthermals, and those that do exist are
49 typically of relatively lower fidelity compared to marine records (e.g. Hesselbo & Pieńkowski
50 2011; Abels et al., 2012). The paucity of high fidelity terrestrial archives hinders our ability
51 to define the response of continental ecosystems and hydrology to ancient warming.

52 The lacustrine sedimentary rock record preserved in the Boltysch Impact Crater, Ukraine
53 (Jolley et al, 2010, 2013; Gilmour et al., 2013) preserves one such high fidelity record of the
54 early Danian Dan-C2 hyperthermal event (~65 Ma). Here, evidence for the impact of the
55 Dan-C2 hyperthermal event on plant ecosystems is examined, and uncoupled from evidence
56 for orbital (Jolley et al., 2015) and solar forcing.

57

58 **The Boltysch Impact Crater record of the Dan-C2 hyperthermal event**

59 In the 0.5 my following the Cretaceous/Palaeogene (K/Pg) boundary, ~400m of sediments
60 were deposited in the Boltysch Impact Crater lake (48.9°N 32.25°E Figure 1) at rates of ~0.8
61 mm y⁻¹, creating a globally unique and detailed record of the early Danian Earth system
62 (Figure 2). Initial investigations of the cores recovered from drilling the crater sediments in
63 2008 (Hole 42/11) identified a unique record of both the K/Pg transition and the Dan-C2
64 hyperthermal event (Jolley et al., 2010; 2013, 2015; Gilmour et al., 2013; 2014). What
65 makes the Boltysch Crater record of fundamental importance is that it records the Dan-C2
66 hyperthermal event at a resolution comparable to modern lake sediments Gilmour et al.,
67 2013, 2014, (Figure 2). Moreover, it is the only non-marine record of this event yet studied.
68 Through our previous analyses (Gilmour et al., 2013; 2014; Jolley et al., 2015), coupled with
69 work by others on marine records of the Dan-C2 event (Quillévéré et al., 2008; Coccioni
70 et al., 2010), it has been established that there are similarities between the Dan-C2 and the
71 PETM and early Toarcian hyperthermals. Notably, all three events are characterised by
72 transient negative C-isotope excursions (CIEs) likely associated with the emission of large
73 amounts of ¹²C, and pronounced warming (Gilmour et al., 2013; Kemp et al., 2005; Zeebe &
74 Zachos, 2013; Hesselbo et al., 2000; Quillévéré, 2008). Additionally, all three CIEs appear to
75 have been paced at least in part by orbital forcing, and coincided with episodes of large-

76 scale volcanism (Gilmour et al., 2013, 2014; Kemp et al., 2005; Lunt et al., 2011). Unlike
77 marine records of the Dan-C2 event, the Boltysch CIE resembles the form of the most
78 detailed records of the Toarcian and PETM (Jolley et al., 2015). However, in comparison to
79 these better-known hyperthermals, the Boltysch Dan-C2 CIE occurs in often laminated, un-
80 bioturbated sediments that are close to an order of magnitude thicker than the most
81 expanded Toarcian and PETM records (Figure 2).

82 A previously published C-isotope record (Gilmour et al., 2013) through the Dan-C2 in
83 Boltysch revealed a negative excursion of $\sim 3\%$ in bulk organic matter spanning ~ 200 m of
84 strata (Figure 2). Statistically significant ($>99\%$ confidence level) ~ 30 m cycles were
85 recognized (Figure 2) in these raw C-isotope data (Gilmour et al., 2013). Based on
86 correlation to marine records, these cycles were attributed to the influence of either
87 precession (~ 21 ky) or obliquity (~ 40 ky) orbital forcing (Gilmour et al., 2013; see also
88 Gilmour et al., 2014). Variations in palynoflora through the Boltysch record have been
89 interpreted as a sequence of moisture availability cycles (MAO's; Jolley et al., 2013, 2015),
90 which occur at a frequency comparable to the cyclicity observed in the carbon isotope
91 record (Jolley et al., 2015 and Figure 2). These MAO's represent alternation between
92 winterwet (warmer, dryer) and mesic forest (cooler, wetter) vegetation biomes.

93 Further temporal constraint on these cycles and the succession has recently become
94 available from a pilot study of sedimentary rock palaeomagnetism, which has established the
95 approximate position of the C29r/C29n magnetic reversal in the Boltysch core (Figure 2).
96 These data corroborate the earlier correlation of Gilmour et al. (2013, 2014) of the Boltysch
97 CIE with the marine Dan-C2 event, and demonstrate that the Boltysch strata span ~ 1 my of
98 the early Danian from the K/Pg (66.00 Ma; 66.043 ± 0.043 in Sprain et al. 2015, see also
99 Dinares-Turell et al., 2014) to within C29n (Figure 2). The base of C29n (65.832 ± 0.036 ,

100 Sprain et al., 2015) has been positioned by our palaeomagnetic analysis and by correlation
101 to records from holes DSDP 528 and DSDP 527 (Quillévéré , 2008, Figure 2) and occurs
102 within Stage 3 of the Boltysh CIE (Figure 2). Comparison to the record of MAO's in post
103 K/Pg boundary Chron 29r sediments of the Boltysh crater fill (Jolley et al.,(2015) identified
104 eleven cycles from the K/Pg boundary to the base of C29n. Using isotopic dating of the
105 K/Pg boundary and of the base of C29n (Sprain et al., 2015) the post K/Pg C29r interval is
106 ~211ky. This duration is in accordance with that proposed by Dinares-Turell et al. (2014
107 and Figure 2). Eleven MAO's have been recognized over the K/Pg boundary to base C29n
108 interval in the Boltysh 42/11 palynology record (Figure 2). Accordingly, ascribing MAO's to
109 21ky solar cycles yields a duration of ~231 ky (21ky x 11 MAO cycles) for this interval, in
110 close agreement with Sprain et al. (2015) (Figure 2). Similarly, the interval from the
111 inception of the Dan-C2 CIE to the base of C29n spans approximately six ~30 m cycles in
112 C-isotopes (Gilmour et al., 2013) providing a similar age calibration.

113

114 **Assessing the nature and rate of ecosystem change**

115 Stratigraphically abrupt composition changes were recorded in the Boltysh palynofloral data,
116 particularly at boundaries between the MAO's (Jolley et al., 2015). Given the time
117 constraints outlined above, these compositional shifts are interpreted as responses to ~21
118 ky orbital precession forcing, showing a correlation with the carbon isotope cyclicality
119 presented by Gilmour et al., (2014). Notably, one of these compositional shifts occurs
120 coincident with the inception of the Dan-C2 CIE. Importantly, this rapid shift in palynofloral
121 composition at the MAO4/MAO5 boundary spans a fraction of a ~21 ky cycle, and hence
122 records a rapid response to climatic change at a sub-orbital, and perhaps anthropogenic-
123 scale, tempo.

124 To assess the potential for using the Boltysch Dan-C2 record to inform our understanding of
125 vegetation and climate change at potentially human-relevant timescales, it was necessary to
126 carry out palynofloral and geochemical investigations at a temporal resolution beyond that
127 derived from the ~1m spaced sample data of Jolley et al (2015). Thus, a new sample set was
128 collected at 0.3 m intervals and analysed for palynofloras and organic C-isotopes. Deriving a
129 multi-centennial record from these samples was targeted at elucidating plant ecosystem
130 dynamics across the boundaries between MAO's and between the wet-cool to warm-dry
131 intervals within the ~21 ky MAO cycles. To obtain a record with a decadal resolution
132 comparable to anthropogenic change, four further intervals of finely laminated sediment
133 were sampled at 0.05 m – 0.06 m spacing. Finally, a single interval of 96 consecutive sub-mm
134 laminations were separated and subjected to palynological analysis (Figure 3). All samples
135 were processed following the methodology outlined in Jolley et al (2015), with the addition
136 of an exotic spore standard and aliquot slide mounts.

137

138 **Vegetation dynamics at MAO Boundaries**

139 Palynological analysis of 0.3 m spaced samples from the later, dryer phase of MAO4,
140 throughout MAO5 into the early wetter phase of MAO6 recovered a rich and diverse
141 palynoflora (Figure 3), consistent with other terrestrial early Danian successions (Jolley et
142 al., 2015; Daly & Jolley, 2015). Pollen and spores dominate the palynofloras, but
143 chlorophycean algae are also present, particularly in the dryer phases of MAO4 and MAO5.
144 Acquisition of these data has allowed comparison of the rate and magnitude of change at
145 both the MAO4/MAO5 boundary (coincidental with the CIE inception, Gilmour et al.,
146 2013), and at the MAO5/MAO6 boundary within the isotope excursion (Figure 3)

147 Following normalization and data reduction (removal of taxa comprising <10% of total
148 flora), the palynofloral data were subjected to detrended correspondence analysis (DCA).
149 Results of this analysis were used to define groups of taxa with similar spatial distributions
150 (Figure 3 and online data). The ecological significance of these groupings was assessed with
151 reference to their botanical affinity and to previous ecological analyses (Jolley et al., 2015).
152 Similar to previous analyses of the entire section (Jolley et al 2015), moisture availability and
153 land surface temperature are reflected in the first two axes of this analysis.

154 Stratigraphical plots of the DCA derived communities from analysis of the 0.3 m spaced
155 data showed apparently rapid ecological turnover at the boundaries between MAO4 and
156 MAO5. A major compositional shift from dominance by mesic communities (Mesic Forest
157 and Mesic Swamp groupings) to dominance by winter wet communities (mid succession
158 Normapolles, Normapolles 1 and Normapolles 2 groupings) occurs over 30cm (480.9m to
159 481.2m). A subsequent comparable period of rapid change was identified at the MAO 5 –
160 MAO6 boundary (Jolley et al., 2015), where a similar shift in palynofloral composition
161 (Figure 3) occurs over 0.3 m (454.19m – 454.49m). The relative significance of these
162 changes was tested using changepoint analysis (Gallagher et al, 2011: Supplementary online
163 data) on DCA axis 1.

164 DCA of the 0.3 m data set revealed short frequency (~2.5 m) oscillations reflecting changes
165 in moisture availability and diversity (Figure 3). Each cycle comprises a cooler, wetter early
166 phase characterized by mesic forest taxa and lower DCA axis 1 values, followed by a later
167 dryer and warmer phase characterized by savanna assemblages. Spectral analysis (2π
168 multitaper) indicates cyclicity in the DCA axis 2 data with a period of ~2.6 m (Figure 3).
169 Considering the orbital chronology, the approximate duration of these cycles is ~2 ky (~12
170 cycles per 30 m precession (21 ky) cycle), and thus potentially consistent with solar

171 Hallstatt cycles (~2.1-2.5 ky period; within the bandwidth error of the observed DCA axis 2
172 cycle period) (e.g. Damon and Sonett, 1991; Kern et al., 2012; Lenz et al., 2016). Also
173 evident from the frequency plots of ordination groups (Figure 3) are intervals of rapid and
174 significant change in palynofloral composition. These are also indicated from changepoint
175 analysis (Supplimentary data) which shows the ~21 ky precession cycles, as well as shorter
176 periodicity changes spanning approximately four ~2.5 m cycles. These unknown ~8 ky
177 periods do not display clear cyclicity in their palynofloras, the boundaries within 21 ky cycles
178 marking shifts to lower moisture availability floras. Both the 21 ky and ~8 ky shifts in
179 palynofloral composition are not necessarily evidence of abrupt changes in climate or
180 forcing. Instead, they represent two different magnitudes of shift in parent flora ecology
181 where cumulative forcing overcame plant community resilience to environmental change.
182 The relative magnitude of these shifts is most readily apparent from the projection of the
183 data on a time axis (Figure 4), highlighting the potential correlation of rapid palynofloral
184 compositional shifts to hypothetical forcing.

185

186 **An anthropogenic-scale record of vegetation change**

187 While data derived from the 0.3 m spaced samples across the inception of the Dan-C2 CIE
188 has enabled identification of second (~8 ky) and third (~2 ky) order oscillations, these data
189 are still of insufficient resolution to elucidate vegetation change at a rate comparable to
190 anthropogenic climate forcing. Repeated intervals of the core, however, are composed of
191 laminated organic-rich mudstone, and this has permitted high fidelity, closely-spaced
192 sampling. Accordingly, four intervals were selected with sample spacing adjusted based on
193 recognition of preliminary thicknesses of the ~2 ky units, varying between 0.05 m and
194 0.06m. Two intervals were chosen from the later stage of MAO4 and MAO5, one

195 immediately following the MAO5 lower boundary, and one at the MAO5 midpoint (Figure
196 3). These were selected to allow the comparison of data from prior to and after the CIE
197 inception, and to allow comparison of sections within the higher moisture availability mesic
198 interval of MAO5 with the winter wet, moisture limited intervals of MAO4 and MAO5
199 (Figure 3).

200 Analysis of these samples yielded data with a conservative species composition, showing
201 little taxonomic variation (Figures 5-8). Within each of the four 0.05 m – 0.06 m spaced
202 sample intervals, the normalised palynological data yields a shared pattern of taxon
203 distribution and abundance. All sections display fluctuations in the abundance of pine and
204 swamp cypress pollen (*Pityosporites haplox* and *Inaperturopollenites hiatus*) with increasing
205 frequencies of the Normapolles pollen *Subtriporopollenites anulatus* subsp. *anulatus*. reflecting
206 a shift from higher to lower moisture availability. Although the 0.05 m – 0.06 m sampled
207 intervals are from relatively wetter/cooler and dryer/warmer intervals of MAO4 and MAO5,
208 the lack of any significant compositional change supports an interpretation of plant
209 ecosystem stability and conservatism at sub-centennial scales.

210 This analysis was performed on intervals in the upper sections of the ~2 ky putative
211 Hallstatt cycles, because they comprise successions of sub-mm laminated mudrocks. The
212 lower intervals of the ~2ky cycles are composed of series of thin fining-upwards deposits
213 (Figure 3), which are probably the lithological equivalent of the wetter-dryer cycles in the
214 laminate palynofloras. Combining the sedimentary cycles with the palynology data from the
215 younger mudrock interval of each ~2 ky cycle suggests a frequency of 9 to 10 cycles per
216 ~2ky, i.e. ~200 y recurrence. Variability at this scale is consistent with solar DeVries/Suess
217 cycles (De Vries, 1958; Suess, 1980, Damon and Sonett, 1991; see also Lüdecke et al.,
218 2015). Although invoking a solar forcing mechanism for these vegetation oscillations is

219 speculative, the data at least confirm that the palynological data from these intervals is likely
220 recording changes at a tempo comparable to anthropogenic climate forcing.

221

222 **Laminations**

223 A further data set gathered from 96 consecutive laminations taken at 464.83 m (Figure 3)
224 show similar patterns in taxon frequency changes and associations as recorded in the 0.05 –
225 0.06 m sampled intervals. Decreasing taxonomic diversity over groups of consecutive
226 laminations are reflected in the standard deviation of the dataset (Figure 9). Boundaries
227 between lamination packages are picked out by an abrupt increase in diversity, and have
228 been used to define oscillations. Variance in the numbers of laminations within each
229 oscillation are in part caused by laboratory constraints on separating the laminations prior
230 to palynological processing, and potentially by depositional or erosional factors. Despite
231 these constraints, spectral analysis of palynomorph density (specimens/g) data indicates a
232 cyclicity with a period of ~12 laminae (10-14 taking into account the bandwidth error,
233 Figure 9).

234 Within each of these lamination-scale oscillations (Figure 9) the oldest interval is dominated
235 by *Tricolpites cf hians* (Platanaceae) and *Inaperturopollenites hiatus* grading up-section into
236 dominance by *Subtriporopollenites anulatus* subsp *anulatus* through the middle and upper
237 intervals of each cycle. This gradation is reflected in a shift from higher diversity to lower
238 diversity and lower dominance flora, reaching a minimum diversity in the youngest interval
239 of each oscillation. This pattern of species distribution and changes in diversity and
240 dominance reflect short duration transitions between mesic floras and 'savanna' type
241 vegetation of the kind seen in the ~2 ky cycles. Preliminary examination of petrographic
242 sections of the laminations in this section of the core indicate that they are probably

243 seasonal couplets (Ebinghaus et al., 2017). The distribution of the palynofloras within the
244 cycles identified does not clearly reflect seasonality, potentially due to taphonomic factors
245 and physical difficulties of laminate separation prior to palynological processing.
246 Nevertheless, the spectral analysis does support the possibility that oscillations observed in
247 this series of consecutive laminations are attributable to ~11 y Schwabe solar cycles (e.g.
248 Damon and Sonett, 1991; Figure 8). Evidence supporting the preservation of these cycles in
249 geological archives is rare (e.g. Weedon et al., 2003), and indeed only the lower part of the
250 analysed interval seems to show oscillations at this period (Figure 8). Nevertheless, Ripepe
251 et al. (1991) documented evidence for Schwabe cycles in varve thickness data in the
252 similarly organic-rich lacustrine shale of the Eocene Green River Formation.

253

254 **Evidence for critical shifts in plant Ecosystems**

255 The abrupt shift in the composition of the palynofloras at the boundaries between MAO4
256 and MAO5 and between MAO5 and MAO6 is the most notable feature of the 0.30m spaced
257 palynofloral data set (Figures 3, 4). Changepoint analysis (Supplementary data 2) of the DCA
258 axis 1 data, alongside plots of mesic to winterwet ratios and the composition of the DCA
259 groups all indicate rapid shifts in floral composition. Winterwet biome taxa are replaced as
260 the dominant group by mesic taxa at 480.9m (MAO 4/MAO 5 boundary) within the 0.30m
261 sample spacing (Figure 4). A second, similarly rapid compositional change is seen at 454.49m
262 (MAO5/MAO6 boundary) where winterwet groups are again replaced as the dominant
263 taxon within 0.30m (Figure 43). Change of this magnitude between samples could infer that
264 this shift in composition took place over ~116 to~175 y, the average duration of sample
265 spacing in ~2 ky cycles 4.12 and 5.1 respectively (Figures 3,4). The sediments at the base of
266 MAO 5 boundary are poorly sorted turbiditic sandstone deposited as a single event (Figure

267 3), which, taken together with the presence of putative ~200 y oscillations in the 0.05 m -
268 0.06 m sample data adjacent to this interval (Figures 5 and 6), supports change in <200 y.
269 While this is an order of magnitude longer than some of the examples of regime shift in the
270 record of modern ecosystems (Reid et al 2015, Capon et al., 2015), elements of floral
271 inertia (Jolley et al., 2015) in the Danian plant ecosystems (rather than the algal systems
272 considered by the aforementioned authors), highlight this as a regime shift event. At the
273 temporal resolution considered here, the response times of individual species to forcing will
274 place a finite limit on the record of palynofloral change. Time taken to reproduce and
275 deposit significant frequencies of pollen/spores to the record may be several decades in
276 mesic woodland, although considerably shorter in shrub/herb dominated savannah. While
277 this inertia would slow the apparent transition from winterwet to mesic communities, any
278 transition from mesic to winterwet communities resulting in plant death would appear more
279 rapid. This is probably illustrated at the ~8 ky oscillation boundaries within MAO5 (at 470.6
280 m and 461.0 m), where an apparently stepwise transition to a dryer palynoflora is recorded
281 (Figure 3).

282 Identifying the boundary between MAO4 and MAO5 as a regime raises further questions
283 with regards to evidence for the presence or absence (van Hoof et al., 2008) of ecosystem
284 flickering (Wang et al., 2012) prior to the event. Taking the 0.30 m spaced palynology data,
285 the first axis of the principal components analysis was fitted to a sum of sinusoids line and
286 the residuals expressed as raw and loess smoothed plots (Figure 10). These plots
287 summarise the degree of compositional fluctuation between mesic and winterwet states.
288 Most notably, the amplitude of fluctuation increases in the four ~2 ky (Hallstatt) cycles prior
289 to the MAO4/MAO5 and MAO5/MAO6 boundaries. Compositional fluctuation of this
290 nature is comparable to flickering in modern ecological systems. In the case of the Boltsh
291 crater flora, the onset of flickering may be related to the phase of the precession cycle:

292 winterwet florals adapted to maximum radiative forcing (Figure 4) become increasingly
293 unstable as forcing decreases. The shorter frequency fluctuations between mesic and
294 winterwet community states may reflect forcing from Hallstatt solar cycles overprinted on
295 the longer term trend. The MAO4/MAO5 boundary for example is inferred to be on at the
296 mid-point between maximum and minimum forcing, resulting in increasing moisture
297 availability and cooler climatic conditions (Figures 4 and 10). Modification of this forcing by
298 solar cycles resulted in increasingly extreme compositional fluctuations in the parent
299 vegetation, prior to reaching a tipping point. On reaching the tipping point, the shift from a
300 winterwet biome to a stable ecological state in a mesic forest biome occurred in <200 y.

301

302 **Uncoupling orbital and solar forcing from hyperthermal impact on vegetation** 303 **communities**

304 The Dan-C2 CIE likely represents a massive input of ¹³C-depleted carbon into the ocean and
305 atmosphere, making it genetically similar to other CIE records (Gilmour et al., 2013). While
306 a good deal of debate is beginning to focus on the rate of climate change associated with
307 these levels of ¹³C-depleted carbon, the high resolution palynofloral data from the Boltys
308 record questions the efficacy of carbon release at the Dan-C2 in driving rapid vegetation
309 community change. From analysis of vegetation community dynamics in this study, it has
310 been possible to identify the impact of orbital and perhaps solar forcing in driving climate
311 change at decadal to centennial scales. However, it is clear that sedimentary depositional
312 system, plant communities, and climate all show slower changes that are correlative with the
313 Dan-C2 isotope excursion (Gilmour et al., 2013, Jolley et al., 2015). The increasing
314 dominance of the thermophilic Normapolles group and the corresponding decline in
315 pteridophyte spores and temperate angiosperm taxa in the CIE Stage 2 supports an

316 increasingly warm and dry climate (Gilmour et al., 2013; Jolley et al., 2015). The dislocation
317 between the changes in palynofloras consequent on orbital and solar forcing, and the change
318 consequent on an overall climate warming from the hyperthermal event is one of tempo.
319 This is illustrated by the high resolution $\delta^{13}\text{C}$ record presented here (Figure 3), using 0.30 m
320 spaced samples. Although exhibiting significant fluctuations, the 1 m sample spaced data of
321 Gilmour et al., (2013) and the 0.30 m spaced loess smoothed C-isotope data are similar and
322 show an increasingly negative trend over the period spanning the winterwet phase MAO4 to
323 winterwet phase MAO 5 of $\sim -3\text{‰}$. This change is reflected in a minor shift between the
324 warmer/dry phase of MAO4 and the warmer/dry phase of MAO5 recorded by the DCA
325 axes plot (Figure 3). A shift is also apparent between the mesic phase of MAO5 and mesic
326 phase of MAO6 (6.2% increase in mean DCA Axis I value) and the winterwet phases of
327 MAO4 and MAO5 (7.8% increase in mean DCA Axis I value). These shifts indicate an
328 increasingly dryer and warmer environment across the CIE inception on a multi-centennial
329 scale. The absence of a rapid negative $\delta^{13}\text{C}$ excursion within these data suggests that, at least
330 in the case of Dan-C2, the increase in atmospheric CO_2 was perhaps a result of a prolonged
331 buildup rather than a single rapid event.

332

333 **Conclusions**

334 Situated near to the northern shores of the Tethyan Ocean, the Boltysch crater lake formed
335 at a paleolatitude of around 30°N (Figure 1). Alternation between mesic and winterwet
336 biomes has been recorded at frequencies consistent with both orbital and solar forcing,
337 with a longer-term overprint of the greenhouse warming impact of the Dan-C2 event.
338 Although the mechanistic link between solar forcing and vegetation remains unclear,
339 perhaps the two most remarkable components of the Boltysch record are the evidence for a

340 'sluggish' CIE inception, and the rapidity of biome regime shift at MAO/~21 ky precession
341 cycle boundaries.

342 Evidence for a gradual onset to the Dan-C2 hyperthermal event, and rapid responses to
343 orbital and sub-orbital forcing indicates that control over the savannah – mesic transition
344 was perhaps derived from the poleward shift of Hadley cell margins. Global warming under
345 greenhouse conditions would be anticipated to bring about a northern expansion of Hadley
346 cells and the down current of stable, dry air migrating north across the study area
347 (Hasegawa et al, 2012; Davis et al., 2016). This would have led to the northern expansion of
348 the savannah, or winterwet biome on the northern shores of Tethys, driving the mesic
349 vegetation belt further to the north. From the repeated alternations between mesic and
350 winterwet biome dominance, it follows that orbital and perhaps solar forcing operated
351 control over the poleward extent of the Hadley cell. Comparable forcing was operated at a
352 slower tempo by the warming and subsequent cooling of the Dan-C2 hyperthermal.

353 In contrast to the suggested collapse of Hadley cells in response to the mid Cretaceous
354 supergreenhouse (Hasegawa et al. 2012), the Boltysh record indicates that the Danian
355 climate retained a subtropical jet zone. Although rapid regime shift happened at the
356 boundary of MAO's/~21 ky cycles there is no evidence to support sudden climate change at
357 these points. Rather, the evidence indicates that when vegetation biomes became
358 unbalanced with respect to climatic change as a consequence of orbital forcing, species
359 were pushed to the limit of their ecological range. The Boltysh vegetation communities in
360 this state were susceptible to collapse, leading to rapid plant community regime shift.

361 Evidence from the Boltysh palynological and carbon isotope record does not support a
362 rapid inception for the Dan-C2 CIE. The high-resolution record (Figures 2, 3) shows a
363 decline of ~4 ppm over ~21 ky. Although this seemingly eliminates this CIE as a deep time

364 proxy record against which to predict the impact of anthropogenic climate change, the
365 impact of orbital and solar forcing on vegetation community dynamics highlights a record of
366 repeated climate warming over decadal and longer scales.

367 With future modelled predictions of climate change indicating a northward expansion of
368 subtropical arid climates away from the equatorial zone (Davis et al., 2016), the Boltys
369 record provides insight into associated vegetation dynamics in a comparable deep time
370 system. Coincidence of solar and orbital forcing with elevated anthropogenic CO₂ have the
371 potential to force regime shift in environmentally stressed plant ecosystems on a decadal
372 scale with consequent societal impacts.

373

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510

511 Figure Captions

512 Figure 1

513 Latest Cretaceous palaeogeographical map of Europe showing the location of the
514 Boltysh impact crater (red circle) at the southern margin of the Fennoscandian
515 landmass on the margins of the Tethyan Ocean (modified from Scotese, 2014).

516

517 Figure 2

518 Stratigraphical framework for the Boltysh 42/11 cored borehole 230m - 581m. The
519 Boltysh bulk organic matter $\delta^{13}\text{C}$ record (Gilmour et al., 2013) is compared to bulk
520 carbonate $\delta^{13}\text{C}$ records from the composite record from a) Zumaia, Spain and ODP
521 hole 1262 South Atlantic (Dinares-Turell et al., 2014) and b) to bulk carbonate $\delta^{13}\text{C}$
522 and $\delta^{18}\text{O}$ records from ODP 1049C, North Atlantic (Quillévéré et al., 2008). The
523 vertical scale for the shorter marine sections is consistent, but because of space
524 constraints, the vertical scale of c) Boltysh 42/11 is reduced by 80%. The position of
525 the K/Pg boundary is at the base of the plotted data for all three sections, while the
526 C29r/C29n boundary is shown for Zumaia and Boltysh. Identification of 'e-bundles'
527 in C29r at Zumaia by Dinares-Turell et al (2014) provides an estimated duration of
528 200-300ky for this interval. Sequence analysis of moisture availability oscillations
529 (MAO's) in the Boltysh palynofloral record by Jolley et al (2015), and of bulk organic
530 matter $\delta^{13}\text{C}$ (Gilmour et al., 2013) identifies up to 11x21ky cycles within the post
531 K/Pg boundary interval of C29r. Isotopic dates for ashes at the K/Pg boundary
532 (66.043 ± 0.043) and the base of C29n (65.832 ± 0.036 , Sprain et al., 2015) indicate a
533 ~211ky interval which is within errors of the duration derived from the MAO cycles
534 of 231ky.

535

536

537 Figure 3

538 Plant community ecology cyclicity across the Dan-C2 hyperthermal excursion
539 inception 490m – 452m 42/11 borehole. Sampled at 0.3m intervals, the
540 stratigraphical plots of DCA derived groups (see supplementary data 1) show the
541 influxes of mesic groups at the base of each ~2ky cycle (horizontal dashed lines) and
542 the rapid switch from savanna to mesic vegetation community dominance at the
543 boundaries between MAO 4/5 and MAO5/6 (bold horizontal dashed lines). This
544 orbital and possible solar cyclicity is reflected in the Axis 1 DCA stratigraphical plot
545 (bold line is loess smoothed) and the power spectrum of linearly interpolated DCA
546 Axis 2 data. Spectrum calculated using multi-taper algorithm (2π) with data linearly
547 detrended and interpolated prior to analysis. Confidence levels (CL) set based on
548 least square fitting of a first order autoregressive (AR1) model to the raw spectrum
549 following methods outlined in Weedon (2003). Spectral peaks exceeding the 99%
550 confidence level at ~1 and ~1.6 cycles per metre are unlikely to be robust since
551 these cycles are each defined by <4 data points (e.g. Herbert, 1994). Filtering
552 conducted using a Gaussian bandwidth filter centred on frequency of 0.39. Note that
553 on the left, the cooler, higher moisture availability intervals of both the ~21ky and
554 ~2ky cycles are shaded blue, passing up into yellow/orange dryer and warmer
555 phases. The position of 0.05m-0.06m spaced sample intervals (see Figures 5-8) and
556 consecutively sampled sub-mm laminations are marked in grey on the left.

557

558 Figure 4

559 DCA axis 1 and DCA ecological group data plotted on a chronstratigraphical axis.

560 This is based on a linear extrapolation of the ~2ky cycles, labelled in grey on the left.

561 Note that the time spacing between 0.3m samples increases in the later, dryer
562 intervals of the ~21ky MAO's reflecting a drop in sedimentation rate in the crater
563 lake. Note the rapid shift from savanna to mesic community dominance at the lower
564 boundaries of MAO5 and MAO6. The synthetic forcing plot on the left of the
565 diagram shows the hypothesised intensity of forcing from the ~21ky precession
566 cycles overlain by ~2ky (hypothetical Hallstatt) cycles. An alternative plot showing
567 the additional forcing potential from the Dan-C2 hyperthermal is shown in red/pink.
568 It is noteworthy that the late stage, savanna dominated floras of MAO4 and MAO5
569 occur during a period of increasing moisture availability, creating environmental
570 stress for the dry adapted plant ecosystem.

571 Figure 5

572 Stratigraphical plot of the dominant palynofloral elements in the 0.05m spaced data
573 set from 484.44m to 483m. The cyclic changes to *Subtriporopollentias anulatus* subsp.
574 *anulatus* dominance in the data set are highlighted with dashed lines. This taxon is a
575 Normapolles group pollen, probably derived from scrub like plants. Because these
576 plants mature relatively rapidly, this may account for the sensitivity evident in the
577 distribution of this taxon in comparison to those derived from what are probably
578 larger arborescent taxa (e.g. *Inaperturopollenites hiatus* derived from Cupressaceae).

579 Figure 6

580 Stratigraphical plot of the dominant palynofloral elements in the 0.05m spaced data
581 set from 476.4m – 475.8m. Horizontal dashed lines denote boundaries between
582 influxes of *Subtriporopollenites anulausl* subsp. *anulatus*.

583 Figure 7

584 Stratigraphical plot of the dominant palynofloral elements in the 0.05m spaced data
585 set from 471.95m – 471.1m. Horizontal dashed lines denote boundaries between
586 influxes of *Subtriporopollenites anulausl* subsp. *anulatus*.

587 Figure 8

588 Stratigraphical plot of the dominant palynofloral elements in the 0.05m spaced data
589 set from 461.65m – 460.0m. Horizontal dashed lines denote boundaries between
590 influxes of *Subtriporopollenites anulausl* subsp. *anulatus*.

591 Figure 9

592 Stratigraphical frequency plot of the palynofloras from 96 consecutive laminations at
593 464.83m. The apparent sensitivity to environmental change implied by the
594 distribution pattern of the platanaceous pollen *Tricolpites cf. hians* indicates that the
595 parent plant was adapted to rapid reproduction, and may have been of scrub or herb
596 physiognomy. The shift to dominance of this taxon in the upper part of the
597 succession is however, probably taphonomic. The horizontal dashed lines mark
598 boundaries between cycles in the data defined by standard deviation of the whole
599 data set. These are supported by a power spectrum of lamina density data showing a
600 clear peak at a period of ~12 laminae. Filtering shows this oscillation is only strong in
601 the lower part of the analysed interval. Filtering was conducted using a Gaussian
602 bandwidth filter centred at the same frequency (i.e. 0.084 cycles per lamina, 0.05
603 bandwidth). Spectrum was calculated using multi-taper algorithm (2π) with data
604 linearly detrended prior to analysis. Confidence levels (CL) were set based on least
605 square fitting of a first order autoregressive (AR1) model to the raw spectrum
606 following methods outlined in Weedon (2003).

607

608 Figure 10

609 Plot of residuals from a sum of sinusoids line fitted to the DCA axis I data shown in
610 Figure 3. The lithological log is as Figure 3. The bold orange line is the loess
611 smoothed plot of the residuals, and shows a close similarity to the mesic to savanna
612 compositional variation that defines the potential Hallstatt cycles with a period of
613 ~2ky. Note the increase in amplitude of the fluctuations with proximity to the
614 MAO4-MAO5 and MAO5-MAO6 boundaries.

615

616 **Jolley et al Supplementary data figure captions**

617 Supplementary data 1: Plot of axis 1 and 2 of the detrended correspondence analysis of the 30cms
618 sample spaced data set between 452m and 489m, borehole 42/11, Boltys meteorite crater,
619 Ukraine.

620 Supplementary data 2: Changepoint analysis of the 30cms sample spaced data borehole 42/11,
621 Boltys crater Ukraine using the approach and software of Gallagher et al. (2011).

622 Supplementary data 3: Photographs of the 42/11 core: a) 462.2m – 457.7m, b) 466.6m – 462.2m.

623 Supplementary data 4: Palynological frequency data for DCA groups in the 30cms spaced data set

624

625

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627