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1 **Reconstructing the reproductive mode of an Ediacaran macro-organism**

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10

11 Enigmatic macrofossils of late Ediacaran age (580–541 million years ago [Ma]) provide the  
12 oldest known record of diverse complex organisms on Earth, lying between the microbially-  
13 dominated ecosystems of the Proterozoic and the Cambrian emergence of the modern  
14 biosphere.<sup>1</sup> Among the oldest and most enigmatic of these macrofossils are the  
15 Rangeomorpha, a group characterized by modular, self-similar branching and a sessile  
16 benthic habit.<sup>2,3,4</sup> Localized occurrences of large *in situ* fossilized rangeomorph populations  
17 allow fundamental aspects of their biology to be resolved using spatial point techniques.<sup>5</sup>  
18 Here, we use such techniques to identify recurrent clustering patterns in the rangeomorph  
19 *Fractofusus*, revealing a complex life history of multigenerational, stolon-like asexual  
20 reproduction, interspersed with dispersal of waterborne propagules. Ecologically, such a  
21 habit would have allowed for both the rapid colonisation of a localized area and transport to  
22 new, previously uncolonized areas. The capacity of *Fractofusus* to derive adult morphology  
23 via two distinct reproductive modes documents the sophistication of its underlying  
24 developmental biology.

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25 Late Ediacaran sedimentary strata (~580–541Ma) of Newfoundland and the UK are  
26 dominated by rangeomorphs, whose unique self-similar branching construction<sup>3</sup> makes  
27 resolution of their phylogenetic relationships, or even their basic biology, difficult.<sup>1</sup> The  
28 occurrence of rangeomorphs in conspicuously deep-water sediments has led to a general  
29 consensus that they were heterotrophic,<sup>6</sup> while the global distribution of charniids (a  
30 rangeomorph sub-group) has been interpreted as evidence for reproduction via waterborne  
31 propagules.<sup>7</sup> In the present study we use spatial statistics and modelling<sup>5,9</sup> in a novel  
32 approach to illuminate the reproductive biology and underlying ecology of one of the most  
33 abundantly-preserved rangeomorph fossils, *Fractofusus*.<sup>8</sup>

34  
35 We analysed three large bedding-plane assemblages of *Fractofusus* in SE Newfoundland: 1)  
36 the ‘D’ surface and 2) the ‘E’ surface at Mistaken Point, Avalon Peninsula;<sup>8,10</sup> and 3) the H14  
37 surface on Bonavista Peninsula (locality 14 of Hofmann et al.)<sup>11</sup> (Extended data Fig. 1a-c). A  
38 volcanic tuff directly above the ‘E’ surface has been dated to 565 ±3 Ma,<sup>12</sup> which also  
39 constrains the age of the underlying ‘D’ surface. Regional lithostratigraphic correlations  
40 suggest that the H14 surface is a few million years younger than the Mistaken Point beds.<sup>11</sup>  
41 All three assemblages occur within deep-marine turbidite sequences, with *Fractofusus* fossils  
42 preserved as negative epirelief external moulds in siltstone hemipelagites, cast from above by  
43 volcanoclastic deposits.<sup>6</sup>

44  
45 *Fractofusus* is conspicuously endemic, restricted almost exclusively to southeastern  
46 Newfoundland,<sup>13</sup> where it dominates many macrofossil assemblages.<sup>10</sup> *Fractofusus* has a  
47 rounded, elongate spindle-like morphology, with two (arguably three<sup>2,13</sup>) offset rows of  
48 irregularly alternating, self-similar, subdivided frondlets arranged along a central axis.<sup>2,14</sup>  
49 *Fractofusus* specimens range from 1cm to 42cm in length<sup>2</sup> (Fig. 1a,b); two species have been

50 described, distinguished by their length:width ratios.<sup>2</sup> The ‘D’ and ‘E’ surfaces are dominated  
51 by the elongate form, *Fractofusus misrai* (L/W=3.2, Fig. 1a), whereas the more ovate  
52 *Fractofusus andersoni* (L/W=1.6, Fig. 1b) dominates the H14 surface.<sup>10</sup> *Fractofusus* occurs  
53 in dense benthic populations and exhibits no evidence of motility or current orientation.<sup>2</sup>  
54 Together with nearest neighbour spatial analyses,<sup>10</sup> these observations point to a sessile,  
55 recumbent, benthic mode of life in aggregated communities.

56

57 The spatial positions of *Fractofusus* were mapped to millimetre-scale resolution using  
58 differentiated GPS (Extended data Figs. 1d-f) on the two surfaces at Mistaken Point, and by  
59 tracing specimen outlines onto acetate sheets at H14; significantly, this latter approach also  
60 allowed size data to be recorded (Extended data Fig. 1f). The ‘D’ and ‘E’ surface data were  
61 corrected for tectonic deformation prior to analysis (Extended data Fig. 2).<sup>7</sup> Heterogeneous  
62 Poisson models were used to identify possible distortions arising from differential erosion of  
63 the bedding planes (Supplementary Table 1). Pair correlation functions (PCF) were  
64 calculated to describe the spatial distributions of taxa on each bedding plane.<sup>5</sup> Monte Carlo  
65 simulations<sup>15</sup> and Diggle’s goodness-of-fit test<sup>5</sup> (the p-value  $p_d$ , where  $p_d=1$  indicates a perfect  
66 model fit and  $p_d=0$  indicates no fit), were used to compare the fit of different spatial models  
67 to the data (specifically homogeneous and heterogeneous Poisson models<sup>16</sup> and single and  
68 double homogeneous and heterogeneous Thomas cluster models).<sup>16</sup> PCFs were also used to  
69 describe the spatial distributions of taxa other than *Fractofusus* on the ‘D’ and ‘E’ surfaces.  
70 For the H14 surface, spatial relationships between three distinct *Fractofusus* size classes  
71 (defined in Methods, Extended data Figs. 3a,b) were analysed by calculating partial PCF<sup>5</sup> and  
72 comparing model fit of bivariate shared parents models (SP) with linked cluster models  
73 (LCM).<sup>16</sup> Finally, spatial directionality was investigated by plotting their generalised K-

74 functions<sup>17</sup> from 0° to 360° (isotropy plots), allowing visualisation of the relative directional  
75 positions of specimens (Fig. 3).

76

77 Non-random spatial distributions of sessile organisms, i.e. those that do not exhibit complete  
78 spatial randomness (CSR), can be explained by either extrinsic factors (e.g. environmental  
79 heterogeneities), or intrinsic reproduction.<sup>18</sup> Identifying the processes behind such patterns is  
80 not straight-forward; however, extrinsically-induced patterns are generally best modelled by  
81 heterogeneous Poisson models,<sup>18</sup> which describe randomly distributed points with a non-  
82 uniform density across the sampled area. In contrast, intrinsic processes typically generate  
83 Thomas cluster models,<sup>18</sup> where the points within each cluster have a normal density  
84 distribution centred on a parent point.

85

86 All three populations of *Fractofusus* were found to be significantly aggregated, conforming  
87 closely to homogeneous Thomas cluster models (Fig. 2a). Specimens on the ‘E’ and H14  
88 surfaces are aggregated at two spatial scales, forming clusters of clusters (Fig. 2a,b). On the  
89 ‘E’ surface, this distribution is best modelled by a nested homogeneous double Thomas  
90 cluster model of 23 clusters (radius  $r=0.242\text{m}$ ), each containing 12 smaller clusters  
91 ( $r=0.074\text{m}$ ) of 3 specimens ( $p_d=0.76$ ). The H14 surface distribution is best modelled by a  
92 nested homogeneous double Thomas cluster model of 24 large clusters ( $r=0.237\text{m}$ ), each  
93 containing 6 clusters ( $r=0.079\text{m}$ ) of 8 specimens ( $p_d=0.89$ ). The ‘D’ surface distribution  
94 forms discrete clusters (not clusters of clusters), which are best modelled by a single Thomas  
95 cluster model ( $p_d=0.77$ ) with 338 *Fractofusus* clusters of 3 specimens ( $r = 0.086\text{m}$ ) (Extended  
96 data Tables 1–2). Importantly, the spatial distribution on the ‘E’ surface can also be  
97 modelled by the nested double cluster pattern found on the H14 surface (Fig. 2b) ( $p_d^{Hon}$   
98  $E=0.51$ ), strongly implying the same underlying process for both distributions (Fig. 2b,

99 Extended data Table 3). The spatial distribution of *Fractofusus* on the ‘D’ surface is  
100 conspicuously similar to that seen in the larger specimens on H14 (Extended data Fig. 4e). By  
101 contrast, the spatial distributions of other taxa – *Thectardis*, *Primocandelabrum* and  
102 *Charniodiscus* – exhibit fundamentally different magnitudes and spatial scales of  
103 aggregation, both to each other and to those of *Fractofusus* (Fig. 2b and Extended data Tables  
104 4, 5).

105  
106 The close fit of *Fractofusus* spatial distributions to single and nested double Thomas cluster  
107 models strongly suggests that they derive from reproductive rather than extrinsic  
108 (environmental) factors. Reproductive biology is further corroborated by size analysis of the  
109 *Fractofusus* population on the H14 surface (Fig. 2c, Extended data Figs. 4a,c,d), which  
110 reveals strikingly different spatial patterns for each of the three size classes (Fig. 2c,  
111 Extended data Tables 1–2). Whereas the largest size class (>11.0cm) is randomly distributed  
112 ( $p_d=0.30$ ), both the intermediate (5.5–11.0cm) and smallest (<5.5cm) size classes are  
113 hierarchically clustered: small individuals cluster around intermediate individuals  
114 ( $p_d^{LCM}=0.74$  versus  $p_d^{SP}=0.03$ ; Extended data Table 5), which in turn cluster around large  
115 individuals ( $p_d^{LCM}=0.66$  versus  $p_d^{SP}=0.01$ ). In other words, the smallest specimens form  
116 clusters (homogeneous nested double Thomas cluster model ( $p_d=0.72$ )) around intermediate-  
117 sized specimens (homogeneous single Thomas cluster model;  $p_d=0.51$ ), which are themselves  
118 clustered around randomly distributed large specimens (homogeneous Poisson model  
119  $p_d=0.31$ ; Figs. 2c, 4, Extended data Fig. 5, Extended data Tables 1–2). Moreover, the  
120 isotropy plots for H14 (Fig. 3) show strong directionality for the large size class, but limited  
121 directionality for the medium and small size classes. The nested clusters on the ‘E’ and H14  
122 surfaces suggest three generations, while the single clusters on the ‘D’ surface suggest two,  
123 reflecting an earlier stage in population development. The difference is consistent with the

124 suggestion that the ‘D’ surface records an earlier stage in the ecological succession of  
125 Ediacaran macroscopic communities<sup>10</sup> (SI:2:3).

126

127 As with other Ediacaran macrofossils, there is no direct fossil evidence of reproductive habits  
128 in *Fractofusus*, but its recurrent distribution on bedding surfaces provides a statistically  
129 robust approach for inferring the underlying processes.<sup>19</sup> In modern oceans, large sessile  
130 organisms typically reproduce by means of waterborne propagules, fragmentation/budding,  
131 and/or stolons (i.e., production of asexual clones that are at least initially connected to the  
132 parent by specialized outgrowths).

133

134 Spatial distribution of waterborne propagules – including both sexual and asexual spores, as  
135 well as sub-millimetre buds and fragments – are a function of current and rate of sinking.  
136 Even with rapid sinking ( $\sim 1\text{mm/s}$ )<sup>20</sup> and slow currents ( $\sim 1\text{cm/s}$ ), propagules released from  
137 the dorsal surface of a ‘parental’ *Fractofusus* ( $\sim 2\text{--}3\text{cm}$  above the substrate) would have been  
138 current aligned<sup>21</sup> and dispersed by decimetres or more.<sup>22</sup> Slow descent times also correspond  
139 with right-skewed (mean greater than the median) density distributions.<sup>20,21</sup> The random  
140 spatial distribution of the H14 largest size class likely reflects a large dispersal distance  
141 (Extended data Table 1), which coupled with its highly directional isotropy plot (Fig. 3a)  
142 indicates that the largest specimens were strongly influenced by currents (c.f. Darroch et  
143 al.<sup>7,10</sup>) As such, they likely derive from waterborne propagules and represent the initial  
144 establishment of a *Fractofusus* population on this surface.

145

146 The hierarchically clustered bedding plane distributions of small and medium *Fractofusus* on  
147 H14 closely match patterns exhibited by organisms reproducing asexually via stolon-like  
148 lateral extensions (Extended data Fig. 5).<sup>23</sup> Cluster distributions of the small and medium

149 size classes are also highly left-skewed (median greater than the mean), with the mean  
150 distance from each “parent” to their “offspring” on the order of a few centimetres (Fig. 2a),  
151 and offspring exhibiting no significant directionality or current orientation (Fig. 3b–c,  
152 Extended data Fig. 3c). The reproducibility of the model distributions across the three  
153 bedding-plane assemblages further attests to the indifferent effects of current: the spatial  
154 distributions of non-tethered offspring would result in patterns dependent on current velocity,  
155 which are unlikely to be consistent across multiple bedding planes in different localities.  
156 Moreover, there are no recorded instances of buds or fragmentary specimens of *Fractofusus*  
157 in any of its 5000+ documented specimens<sup>1,10,11,24</sup> (see SI:2.5, SI:3). As such, the  
158 *Fractofusus* clusters on the H14 surface are not consistent with waterborne propagules or  
159 fragmentation/budding, but are directly comparable to stolon-like reproduction. Other taxa  
160 exhibit an intriguing range of non-random habits, and our preliminary analyses indicate that  
161 *Primocandelabrum* and *Charniodiscus* may have also reproduced using stolons.

162

163 Reproductive biology lies at the core of ecological and evolutionary dynamics, and its  
164 positive identification in Ediacaran microfossils has the potential to illuminate the beginnings  
165 of the modern marine biosphere. Previous studies of Ediacaran microfossils have  
166 investigated the seasonality of reproduction<sup>7</sup>, identified putative stolons<sup>28,29</sup>, and inferred  
167 sexual or asexual reproduction based on biogeographic distribution or qualitative description  
168 of local populations.<sup>7,10</sup> In the case of phosphatized ‘embryo’ microfossils, internal cell  
169 packages have been interpreted as evidence of germ-soma differentiation,<sup>30</sup> but it remains to  
170 be seen how those fossils relate to the evolution of large and/or complex eukaryotes.

171

172 The identification in *Fractofusus* of a multigenerational asexual clonal phase, interspersed  
173 with the release of waterborne propagules, is the first statistically robust account of



174 reproductive life history reported in an Ediacaran macrofossil. Such a strategy would have  
175 allowed for the rapid exploitation of localized areas, as well as for transport to new,  
176 previously uncolonized areas. The conclusion that *Fractofusus* could switch between  
177 reproductive modes further reveals the sophistication of its underlying developmental  
178 programme, capable not only of tissue differentiation, but also the generation of new  
179 macroscopic individuals from both benthic stolons and waterborne propagules.

180

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257

258 **Supplementary Information** is linked to the online version of the paper at

259 [www.nature.com/nature](http://www.nature.com/nature).

260

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266 Readers are advised that access to both of the aforementioned fossil localities is by scientific  
267 research permit only. Contact the relevant Department listed above for further information.  
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273

#### 274 **Author Contributions**

275 E.G.M conceived the project, collected data on the ‘D’ and ‘E’ surfaces and ran the analyses.

276 C.G.K, A.G.L and J.J. M collected data on the H14 surface. All authors discussed the results  
277 and prepared the manuscript.

278

#### 279 **Author Information**

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281 declare no competing financial interests. Correspondence and requests for materials should  
282 be addressed to E. G. M. ek338@cam.ac.uk.

283

284 **Figure 1: a**, *Fractofusus andersoni* specimen from the H14 surface. **b**, *Fractofusus misrai*  
285 from the ‘E’ surface, showing a large size-class partial specimen (~20cm, above) alongside a  
286 small size-class specimen (3.5cm in length, below). Scale bars = 1cm. Photographs are  
287 unretrodeformed.

288 **Figure 2:** PCF for mapped taxa. For all plots the x-axis is the inter-point distance between  
289 organisms in metres. The y-axis PCF=1 indicate CSR, <1 indicates segregation, and >1  
290 indicates aggregation. **a**, PCF for *Fractofusus* on the ‘D’ surface (1040 specimens), ‘E’  
291 surface (1141 specimens) and H14 surface (1214 specimens). Grey shaded area depicts the  
292 bounds of 99 Monte Carlo simulations of CSR. Since the PCF curves are not completely  
293 within these areas, the CSR hypothesis is rejected and one can assume that the *Fractofusus*  
294 distributions on all three surfaces form cluster patterns ( $p_d^D < 0.01$ ,  $p_d^E < 0.01$ ,  $p_d^{H14} < 0.01$ ). **b**,  
295 PCF for non-CSR ‘E’ surface taxa (charniid 76 specimens, *Charniodiscus* 326 specimens,  
296 *Primocandelabrum* 311 specimens and *Thectardis* 39 specimens). Grey shaded area depicts  
297 99 Monte Carlo simulation of the best-fit H14 surface model of double Thomas cluster  
298 process. Note how the ‘E’ surface *Fractofusus* PCF follows the H14 surface PCF very  
299 closely, and can be modelled by the same process ( $p_d = 0.51$ ). Other ‘E’ surface taxa have  
300 dramatically different PCF to the *Fractofusus* PCF. **c**, PCF for the three size classes of  
301 *Fractofusus* on H14 surface. Grey shaded area depicts the 99 Monte Carlo simulation of CSR  
302 . The large size-class (350 specimens) exhibits CSR ( $p_d = 0.30$ ), the intermediate size-class  
303 (310 specimens) shows aggregation <0.10m (single Thomas cluster model ( $p_d = 0.51$ )). The  
304 small size-class (554 specimens) shows a large aggregation <0.08m and a lesser aggregation  
305 between 0.08m and 0.20m (double Thomas cluster model ( $p_d = 0.72$ )).

306

307 **Figure 3.** Isotropy plots from the H14 surface for each size class of *Fractofusus*, providing a  
308 visualisation of specimen positions relative to one another. The vertical axis on each

309 subfigure depicts the colour map of specimens/m<sup>2</sup> normalised to account for different  
310 densities between size-classes. A peak (<1) is shown in green or yellow and depicts  
311 clustering, while a dip (<1) is shown in blue and depicts segregation. If there are no  
312 directional effects then the colour map in every direction from the centre point should be  
313 similar. **a**, The large size-class shows strong anisotropy, with aggregation of up to 4  
314 normalised specimens/m<sup>2</sup>. In contrast the **b**, medium and **c**, small size-classes show isotropy,  
315 that is a relative evenness of aggregations with a maximum density variation up to 0.5  
316 normalised specimens/m<sup>2</sup>.

317 **Figure 4:** Schematic diagram showing simplified *Fractofusus* spatial arrangements. The  
318 actual number of clusters, and clusters within those clusters, is higher than shown (23 clusters  
319 each containing 12 clusters of 3 specimens on the H14 surface), making their direct visual  
320 detection challenging. No overlapping specimens are shown because, while the best-fit  
321 models allow for overlaps, the observed PCF between the small size-class (Extended data  
322 Fig. 4c,d) and the large size-class (Fig. 2b) shows a small segregation (<3cm) away from the  
323 model behaviour, and a similar, non-significant segregation for the large size-class.

324

## 325 **Methods**

### 326 **Data collection**

327 Fossil taxa<sup>31</sup> and spatial positions on the Mistaken Point 'D' and 'E' surfaces (Extended data  
328 Figs. 1a,b, 2a,b) were recorded using differentiated GPS over a period of fifteen days. A fixed  
329 GPS transmitter was installed on a headland overlooking the bedding planes, and a portable  
330 GPS receiver was used to map 4496 individual fossils over a total area of 123.7m<sup>2</sup> for both  
331 surfaces (SI:2.1); the mean accuracy of data points was 0.4 ±0.06 cm horizontally and 0.82  
332 ±0.11 cm vertically. The measured position of each specimen represents the mean of five  
333 separate GPS readings collected over five seconds; both the accuracy (standard deviation of

334 the five readings) and the associated weather conditions were recorded for each reading.  
335 Mann-Whitney tests were used to compare the densities of specimens recorded in differing  
336 weather conditions, with the null hypothesis that the density should not depend on the  
337 weather conditions on the day of data collection.

338 Fossil positions on the H14 surface, Bonavista Peninsula (Extended data Fig. 1d) were  
339 recorded by tracing the outline of each specimen onto 2m x 5m acetate sheets. Cleavage and  
340 other geological features were also traced. These data were collected by three people, two  
341 holding the sheets in position and the third recording the data. Wind-induced slippage  
342 (affecting large-scale spatial relationships (>0.75 m) for three out of five of the sheets) was  
343 determined by measuring the differences between cleavage features crossing sheets, yielding  
344 a mean accuracy of  $1.47 \pm 0.26$ cm along strike, and  $1.53 \pm 0.08$ cm parallel to dip. Over the  
345 0.5m distance that the PCFs were calculated, these errors translate to  $0.37 \pm 0.26$ cm along  
346 strike and  $0.15 \pm 0.08$ cm parallel to dip – substantially less than the 1cm cells within which  
347 specimen densities were measured to calculate the PCFs (Methods section: Testing for non-  
348 random spatial distribution). The sheet approach was used to map the H14 surface because it  
349 provided size data more efficiently than direct measurement plus GPS.

350

### 351 **Specimen identification**

352 Specimens were recorded as one of twelve taxonomic groups of macrofossils, including two  
353 ‘bin’ groups.<sup>32</sup> : 1) *Bradgatia*, 2) *Pectinifrons*, 3) *Thectardis*, 4) *Fractofusus andersoni* + *F.*  
354 *misrai*, 5) *Charniodiscus spinosus* + *C. procerus*, 6) “Feather Dusters”, 7) *Hiemalora* , 8)  
355 Ivesheadiomorphs,<sup>33</sup> 9) Lobate Discs, 10) *Charnia* ‘A’ + *Charnia* ‘B’ [*Charnia* ‘A’ consists  
356 of *Beothukis mistakenis*<sup>34,35</sup> (which dominates the ‘E’ surface) and *Charnia masoni*.  
357 *Charnia* ‘B’ now reassigned as *Trepassia wardae*.<sup>34</sup> Charniid populations on Mistaken Point  
358 are dominated by *Beothukis* (only four individuals on the ‘E’ surface are true *Charnia*



359 species), therefore direct comparison of data from this grouping with those from other  
360 taxonomic groups should be undertaken with caution. 11) “Holdfast Discs” [all discoidal  
361 specimens of uncertain affinity, with or without associated stems, which lack sufficient detail  
362 to identify the taxon], 12) “Other Species” [rare forms that do not fall into any of the other  
363 groups; e.g., *Hapsidophyllas*].

364

### 365 **Retrodeformation**

366 The tectonically distorted data from the Mistaken Point surfaces were retrodeformed by  
367 returning elongated holdfast discs to a circular outline<sup>6</sup> The ‘D’ surface (based on 13  
368 specimens), showed a deformation factor of  $1.35 \pm 0.11$  ( $R^2 = 0.92$ ), and the ‘E’ surface (based  
369 on 12 specimens )  $1.71 \pm 0.08$  ( $R^2 = 0.754$ ), both within the previously measured range.<sup>10</sup> In  
370 the absence of any obviously directional distortion or suitable deformation indicators,  
371 measurements taken from the H14 locality were not adjusted in this fashion.

372

### 373 **Data Collection Bias**

374 The impact of mechanical weathering on the ‘D’ and ‘E’ surfaces was investigated by  
375 modelling the fossil distributions as heterogeneous Poisson processes. Fossils were originally  
376 covered in a thin layer of volcanic tuff, which has since been partially weathered away to  
377 expose the bedding planes, potentially inducing bias. If the density of a particular taxon is  
378 correlated to modern weathering features, then such processes are likely to be masking the  
379 true palaeontological distribution of the fossils. Initial data exploration and residual analysis  
380 of weathering effects was performed in R<sup>36</sup> using the package spatstat.<sup>37</sup> Four covariates,  
381 corresponding to four potential erosion sources, were investigated:

- 382 1. Across the bedding plane (South to North)  $x$ , which is differentially eroded by cliff  
383 fall and water runoff from a small stream on the northern side for the 'E' surface.
- 384 2. Along the three bedding planes (West to East)  $y$ , which are subject to differential  
385 erosion from wave action.
- 386 3. The south-western corner  $xy$ , which is the first point of contact for most waves on the  
387 'E' surface.
- 388 4. The height of the fossils above the troughs of the tectonic ripples on the 'D' and 'E'  
389 surfaces  $h$ , which is an inverse proxy for ash coverage.
- 390

391 On each bedding plane, and for each parameter, the spatial density of fossils in relation to  
392 the parameter was plotted, along with the best-fit quadratic line. This best-fit line was then  
393 used to model the change of density compared to the covariant. The inhomogeneous models  
394 were tested primarily on the non-retrodeformed data (since retrodeformation may mask any  
395 aggregation due to preservational bias), and verified by conducting similar tests on the  
396 retrodeformed data. Two different methods were used to compare the different  
397 inhomogeneous models: Kolmogorov-Smirnov tests were performed on quadrats of the data  
398 to investigate the distributions relative to the four covariates<sup>38</sup> (Supplementary Table 1), then  
399 the model fit was assessed using the model residuals.<sup>5,9</sup> Model residuals assessed the fit of  
400 the model to the data via plotting Q-Q and smoothed residual plots. If the observed line in the  
401 Q-Q plot falls outside two standard deviations of the model, the model was rejected.<sup>5,9</sup>

402 Akaike information criterion (AIC) values<sup>39</sup> were used to compare the relative quality of the  
403 statistical models that fit the data.

404 Bias generated by differing light conditions was tested by comparing densities of areas  
405 either side of a specific grid line that delineated where one (the right hand) side was mapped  
406 under optimal conditions, and the other under sub-optimal conditions. Similar levels of ash

407 erosion existed on either side of this grid line, so we expected that similar fossil densities  
408 should be found on both sides if the weather did not affect data collection. The densities were  
409 then compared using a Mann-Whitney test.

410

#### 411 **Testing for non-random spatial distributions**

412 Initial data exploration, inhomogeneous Poisson modelling and residual analysis were  
413 performed in R<sup>37</sup> using the package spatstat.<sup>38</sup> Programita<sup>40</sup> was used to find distance  
414 measures and to perform aggregation model fitting (described in detail in references 40-42).  
415 Pair correlation functions (PCF) was used to assess which did not exhibit CSR, where PCF  
416 value reflects how many times more likely the distribution seen is aggregated (or segregated)  
417 compared to CSR as follows:

- 418 1. A distribution map was plotted for individual taxa, with the surfaces split into a grid  
419 of 1cm x 1cm cells, within which the population density was calculated.
- 420 2. The smoothed PCF was calculated with smoothing dependent on number of  
421 specimens for each taxon. A three cell smoothing was applied for *Fractofusus* (D, E  
422 and H14), five cells for *Charniodiscus* (E), *Pectinifrons* (D), *Bradgatia* (D and E) and  
423 *Primocandelabrum* (E) and 15 cells for *Thectardis* (E) and Charniids (D and E).
- 424 3. 99 simulations were run for each taxon on a homogeneous background to generate  
425 simulation envelopes around the random (PCF = 1). 99 simulations were run (instead of  
426 100, for example) so that the  $p_d$  values could be measured in 0.01 increments.
- 427 4.  $p_d$  values were calculated using Diggle's goodness-of-fit test.<sup>15</sup>

428

429 For those taxa found to exhibit excursions outside the simulation envelope, four types of  
430 processes were then fitted to the data: heterogeneous Poisson process, Thomas single cluster

431 processes on both homogeneous and heterogeneous backgrounds, and Thomas double cluster  
432 process. The resulting models were then compared to find the best model for each taxon

433

#### 434 **Complexities of assessing model fit**

435 Testing for significance with spatial point data is more complicated than for classical  
436 statistics due to lack of independence and variety of point pattern distributions<sup>4</sup>. Monte Carlo  
437 simulations provide a good assessment, but the simulation envelope does not necessarily  
438 correspond to a confidence interval,<sup>15</sup> and runs the risk of Type 1 error if the observed PCF  
439 falls near the edge of the simulation envelope.<sup>15</sup> The size of simulation envelopes depends on  
440 the sample size, so that smaller sample sizes (such as the H14 large size class of 350  
441 specimens) has a relatively large simulation envelope in contrast to the ‘D’, ‘E’ and H14  
442 surfaces (all >1000 specimens). A comparatively large simulation envelope reduces the  
443 likelihood that the null model (such as CSR) is rejected. Consequently, hypothesis testing  
444 needs to be further supplemented. We used Diggle’s goodness-of-fit test, which is a single  
445 test statistic<sup>15</sup> ( $p_d$ ) representing the total squared deviation between the observed pattern and  
446 the theoretical result across the studied distances.  $p_d$  was used in conjunction with visual  
447 inspection of Monte Carlo simulations for two reasons. First,  $p_d$  does not strictly test  
448 whether a model should be accepted or rejected, but whether the PCF for the observed data is  
449 within the range of the stochastic realization of the model.<sup>43</sup> Secondly,  $p_d$  depends on the  
450 range over that it is calculated. For example, the model which best describes the ‘E’ surface  
451 data has  $p_d=0.56$ , which may appear low. However, inspection of the PCF (Extended data  
452 Fig. 3b) shows a very close fit to the double Thomas cluster model above 2cm (Extended data  
453 Table 2). The finite size of *Fractofusus* is reflected in the lower PCF values at small  
454 distances, and so the model is only fit >2cm.

455           Interpreting ecological processes from spatial point patterns is imprecise. Different  
456 processes can produce similar spatial patterns,<sup>9,18,44,45</sup> with the complex interplay of intra- and  
457 interspecific interactions affecting organismal distributions.<sup>46,47,48</sup> Even so, application of  
458 complementary statistical techniques, such as pair correlation functions (PCF) combined with  
459 comparisons of inhomogeneous Poisson and Thomas cluster models, and nearest neighbour  
460 distance analysis, offers the most effective means of teasing out the underlying ecological  
461 processes.

462

### 463 **Model fitting**

464 If a taxon was not randomly distributed on a homogeneous background (Extended data Table  
465 1), the random model on a heterogeneous background was tested. Six different heterogeneous  
466 backgrounds were generated, as follows (Extended data Table 4):

467           1. The first heterogeneous background was created from the density map of the taxon  
468 under consideration, being defined by a circle of radius R over which the density is  
469 averaged throughout the sample area. Density maps were formed using estimators  
470 within the range of  $0.1\text{m} < R < 1\text{m}$ , and the R corresponding to the best-fit model was  
471 used.

472           2. The second heterogeneous background was created from density maps of all  
473 specimens on each surface combined.

474           3. The third to sixth heterogeneous backgrounds were created from the four separate  
475 density maps of *Fractofusus*, *Ivesheadiomorphs*, *Charniodiscus* and  
476 *Primocandelabrum*.

477

478 This procedure follows that used to test for a non-random distribution on a homogeneous  
479 background (Section: Testing for non-random spatial distributions), except at point 3, where

480 the homogeneous background on which the taxa were simulated is replaced by a  
481 heterogeneous one. If excursions outside the simulation envelopes for both homogeneous  
482 and heterogeneous Poisson models remained, then cluster models were fitted to the data. For  
483 each non-random taxon, univariate cluster models were fitted as follows (Extended data  
484 Table 1):

- 485 1. The PCF and L function<sup>49</sup> of the observed data were found. Both measures were  
486 calculated to ensure that the best-fit model is not optimized towards only one distance  
487 measure, and thus encapsulates all spatial characteristics.
- 488 2. Best-fit Thomas cluster processes<sup>50</sup> were fitted to the two functions where  $PCF > 1$ .  
489 The best-fit lines were not fitted to fluctuations around the random line of  $PCF = 1$  in  
490 order to aid good fit about the actual aggregations, and to limit fitting of the model  
491 about random fluctuations. Programita used the minimal contrast method<sup>9,15</sup> to find the  
492 best-fit model.<sup>9</sup>
- 493 3. If the model did not describe the observed data well, the lines were refitted using just  
494 the PCF. If that fit was also poor, then only the L-function was used.
- 495 4. 99 simulations of this model were generated to create simulation envelopes, and the  
496 fit checked using the O-ring statistic.<sup>40</sup>
- 497 5.  $p_d$  was calculated over the model range. Very small-scale segregations (under 2cm)  
498 were not included in the model fitting, since they likely represent the finite size of the  
499 specimens, and the lack of specimen overlap.
- 500 6. If there were no excursions outside the simulation envelope and the  $p_d$ -value was  
501 high, then a univariate homogeneous cluster model was interpreted as the best model.

502

503 Taxa exhibiting two scales of clustering were modelled as Thomas double cluster processes  
504 on a homogeneous background, and as single Thomas cluster processes on a heterogeneous  
505 background, as follows (Extended data Table 2):

506 1. The PCF was plotted, and ranges for the two different scales of clustering were  
507 found. For example, the small-scale cluster may be  $0 < r < 0.5m$ , and the large-scale  
508 cluster  $0.5m < r < 1.5m$ .

509 2. The large-scale cluster model was fitted.

510 3. The parameters of the large-scale single cluster model were used as parameters for  
511 the large-scale clusters of the double cluster model.

512 4. Nearest-neighbour functions were calculated and compared to the parameters of the  
513 different-scaled clusters to test for nestedness.

514

#### 515 **Comparison between and within taxa**

516 To assess whether *Fractofusus* spatial distributions could be similarly modelled on all three  
517 bedding planes, the best-fit model from each surface was fitted to the other two surfaces.

518 Simulation envelopes and  $p_d$ -values were used to evaluate fit (Fig. 2b, Extended data Table  
519 3).

520 The uniqueness of each taxon's spatial distribution was assessed by fitting the best-fit  
521 models for high abundance taxa (*Fractofusus*, *Charniodiscus*, *Primocandelabrum*) onto each  
522 other. Low-abundance taxa (Charniids, *Thectardis*) were excluded from this comparison  
523 because they yield large simulation envelopes, and consequently very different models fit  
524 within the generated envelopes.

525

#### 526 **Size classes**

527 The *Fractofusus* size data from the H14 surface permitted investigation of interactions  
528 between *Fractofusus* specimens of different sizes. To determine whether there was a  
529 dependency between spatial distribution and specimen size, the mark correlation function was  
530 calculated<sup>17,51</sup> and compared to the simulation envelope produced from 99 Monte Carlo  
531 simulations (Extended data Fig. 3a).

532 The most objective way to resolve the number and range of size classes in a  
533 population is by fitting size-frequency distribution data (the natural log of the variables-  
534 lengths, widths, and the bivariate case of lengths multiplied by width) to various models,  
535 followed by comparison of (logarithmically scaled) Bayesian information criterion (BIC)  
536 values,<sup>7</sup> which we performed in R using the package MCLUST.<sup>52</sup> The number of populations  
537 thus identified was then used to define the most appropriate size classes. A BIC value  
538 difference of >10 corresponds to a “decisive” rejection of the hypothesis that two models are  
539 the same, whereas values <6 indicate only weakly reject similarity of the models.<sup>59</sup>

540 Once defined, the spatial distributions for each size class were analyzed using the  
541 techniques described in the model fitting section (Methods: Model fitting). Although it was  
542 necessary to set firm boundaries for each size class, the populations are normally distributed  
543 and therefore overlap. As a result, the largest individuals of the small population are grouped  
544 within the middle size class, while some of the smallest of the medium population are  
545 included within the small size class.

546 Using this information, further analyses were performed to consider the spatial  
547 relationships between individual size classes. The PCF between each size class was  
548 determined, and the best-fit shared parent (SP) and linked cluster models (LCM) were fitted  
549 (Extended data Table 5, Extended data Fig. 4c,d), and the fit of each model assessed. SP  
550 models describe the pattern when two clustered size classes both cluster around an (un-  
551 defined) point or area, such as the effect of two different heterogeneous soil effects on tree



552 growth.<sup>53</sup> Linked cluster models arise when one size class clusters around another size class,  
553 for example when tree saplings cluster around their parent.<sup>54</sup> The procedure behind model  
554 fitting was similar to the single group/size class (univariate) case, but instead of single  
555 groupings, two size-classes (bivariate) PCF were used instead:

- 556 1. The best-fit Thomas cluster processes were found for each of the size classes (SP and  
557 LCM).
- 558 2. The single size class parameters for each size were input to the model classes (both  
559 models for the SP model and only the parent model for LCM).
- 560 3. The best-fit model was fitted to the PCF and L functions.
- 561 4. If the model fit was poor (errors >0.025), then the model was fitted using the PCF  
562 and then the L function. If neither were a good fit, then the spatial scale that the model  
563 was fitted to was reduced, so that a good model could be found for at least part of the  
564 spatial scale.
- 565 5. The model was checked using 99 Monte Carlo simulations,  $p_d$ -values, and by  
566 comparing the univariate parameters to the bivariate model parameters.

567

### 568 **Isotropy analysis**

569 To assess whether non-random behaviour was stronger in any particular direction (i.e.,  
570 exhibited isotropy), density plots of the K measure<sup>5, 55</sup> were used to calculate the normalized  
571 density in each direction around each point (Fig. 3 and Extended data Fig. 3c), where  
572 normalized values of 1 indicate random distribution (homogeneous Poisson process), vs <1  
573 (segregation) and >1 (aggregation). The plots are produced by calculating the average of all  
574 the vectors that join all pairs of points over different realisations of the point process. Each  
575 point in turn is positioned on the plot centre, then a vector is drawn to every point. The  
576 resulting vector scatter plot (also known as a Fry plot) is then smoothed.

577

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- 639

640 **Extended Data Figure 1: Map and simplified stratigraphic column showing the position**  
641 **of studied bedding planes with bedding plane maps of *Fractofusus*.** **a**, Newfoundland,  
642 Eastern Canada. Dashed area indicates region of interest in B. **b**, The Avalon and Bonavista  
643 Peninsulas, eastern Newfoundland. Locations of the bedding planes are indicated. **c**,  
644 Stratigraphic column (not to scale) compiled of information from the Avalon and Bonavista  
645 Peninsulas; lithological units in each region are treated as correlative in this study, but work  
646 is ongoing to determine the validity of this assumption. The ‘E’ surface at Mistaken Point has  
647 been dated to  $565 \pm 3 \text{ Ma}^{12}$ . There are currently no available radiometric dates from the  
648 Bonavista Peninsula. Maps of *Fractofusus* positions on **d**, the ‘D’ surface, **e**, the ‘E’ surface  
649 and **f**, the H14 surface. In Fig. e the largest specimens in light blue, medium specimens in  
650 mid blue and smallest specimens in dark blue.

651 **Extended Data Figure 2: Retrodeformation calculations on the Mistaken Point surfaces.**  
652 Plots of the lengths versus widths of discs from **a**, the ‘D’ surface, Mistaken Point and **b**, the  
653 ‘E’ surface Mistaken Point. The gradient of the line defines the retrodeformation factor,  
654 which for ‘D’ surface is  $1.35 \pm 0.11$  ( $R^2 = 0.92$ ), and for ‘E’ surface is  $1.71 \pm 0.08$  ( $R^2 = 0.75$ ).  
655 **c**, *Fractofusus* PCF on the ‘E’ surface with (solid black line) and without (dashed black line)  
656 retrodeformation. The grey shaded area depicts the boundary of 99 Monte Carlo simulations  
657 for the model which provided the best-fit model to the retrodeformed data, which has a good  
658 fit on the non-retrodeformed data ( $p_d = 0.60$ )

659 **Extended Data Figure 3: Size distribution analysis of *Fractofusus* for the H14 surface.**  
660 **a**, Size-frequency distributions for *Fractofusus*, and **b**, the results of Bayesian Information  
661 Criterion<sup>52,53</sup> (BIC) (univariate data). Triangles and squares correspond to models assuming  
662 equal and unequal variance respectively. High BIC values correspond to a good model fit, so  
663 the best-fit model is a three component equal variance model using log-normalized length  
664 data. **c-d**, Rose diagrams plotting the directional orientation of the different size classes of

665 *Fractofusus* on H14 surface showing **c**, Large size class (<11.0cm), **d**, Intermediate size class  
666 (5.5-11.0cm) and **e**, Small size class (<5.5cm). The angles of the *Fractofusus* central axis  
667 relative to North ( $0^\circ$ ). There is no strong orientation preference for any of the size classes.

668 **Extended Data Figure 4: Distance measures for the size data from H14 surface.** For all  
669 plots the x-axis is the inter-point distance between organisms in metres. **a**, Mark correlation  
670 function,<sup>5</sup> where 1 corresponds to a lack of correlation of size, such that *Fractofusus* size is  
671 independent and identically distributed. <1 corresponds to a positive dependency (in contrast  
672 to PCF) and >1 corresponds to a negative dependency. Fig. a shows that small *Fractofusus*  
673 on the H14 surface (<0.3cm) are more likely to be found near each other than expected by  
674 random. **b**, The H14 surface PCF (solid line) showing the model that fits the data best, a  
675 double Thomas cluster model (dotted line,  $p_d=0.89$ ), and the simulation envelope for 99  
676 Monte Carlo simulations (grey shaded area). PCF for the best-fit models for the bivariate  
677 size-classes of *Fractofusus* on H14 surface showing: **c**, Linked cluster model for small with  
678 medium size classes ( $p_d=0.74$ ) and **d**, Linked cluster model for medium with large size class  
679 ( $p_d=0.66$ ). **e**, The PCF of the largest size class of H14 (solid line), showing the CSR Monte  
680 Carlo simulation envelope in grey, with the 'D' surface PCF (dotted line,  $p_d=0.56$ ). **f**,  
681 Nearest neighbour distances (solid line,  $p_d=0.01$ ) with CSR Monte Carlo simulation envelope  
682 in grey.

683

684 **Extended Data Figure 5: Artistic reconstruction of *Fractofusus* on the H14 surface,**  
685 Bonavista Peninsula. Artwork by C.G.K. The bottom right features a large *Fractofusus*  
686 around which there are five to eight medium specimens clustered. Each of the medium  
687 specimens also has small specimens clustered around them. The small specimens therefore  
688 form an independent double cluster pattern, that is, clusters of clusters.

689

690 **Extended Data Table 1: Best-fit univariate cluster models.** For the heterogeneous  
691 backgrounds, the moving window radius is 0.5m using the same taxon density as the taxon  
692 being modelled.  $p_d = 1$  corresponds to a perfect fit of the model on the data, while  $p_d = 0$   
693 corresponds to no fit. The error function of the best-fit model gives the fraction of the total  
694 sum of squares for the transformed empirical PCF which are not explained by the model.

695

696 **Extended Data Table 2: Best-fit univariate double cluster models.** Large-scale clusters  
697 are determined for the univariate cluster then input into the model, and the small-scale  
698 clusters are determined in the double cluster analysis.  $p_d = 1$  corresponds to a perfect fit of the  
699 model on the data, while  $p_d = 0$  corresponds to no fit.

700 **Extended Data Table 3: The best-fit double Thomas cluster models fit onto other taxon**  
701  $p_d = 1$  corresponds to a perfect fit of the model on the data, while  $p_d = 0$  corresponds to no fit.  
702 Note, that while these numbers may seem low (such as the ‘E’ surface fit), they need to be  
703 considered in context of the PCF graph (Extended Data Fig. 2b), which clearly shows a good  
704 fit to the data, with the small fluctuations of the observed PCF around the model PCF.

705

706 **Extended Data Table 4: Best-fit univariate cluster models on heterogeneous**  
707 **backgrounds for ‘E’ surface taxa.** Univariate clusters, either fitted to the small scale (S)  
708 or large scale (L) were modelled on different backgrounds defined by the density map of all  
709 taxonomic groups, or Random for charniid. C: Thomas cluster on homogeneous background.  
710 CH: Thomas cluster on heterogeneous background. For the heterogeneous backgrounds, the  
711 moving window radius is 0.5m since that radius produced the best-fit for Charniids:  
712 Heterogeneous Cluster model on a background density constructed from all species: (CH<sub>all</sub>);  
713 Ivesheadiamorphs (CH<sub>Ive</sub>), *Fractofusus* (CH<sub>Frac</sub>), *Charniodiscus* (CH<sub>Cha</sub>),  
714 *Primocandelabrum* (CH<sub>Primo</sub>). CSR on heterogeneous background (H). *Bradgatia* (H<sub>Bra</sub>),

715 Lobate Discs ( $H_{Lob}$ ), *Thectardis* ( $H_{The}$ ), Charniid ( $H_{Char}$ ).  $p_d = 1$  corresponds to a perfect fit  
716 of the model on the data, while  $p_d = 0$  corresponds to no fit. The H14 surface did not possess  
717 enough non-*Fractofusus* specimens to perform similar analyses. NA: not applicable.

718

719 **Extended Data Table 5: Models for bivariate analysis between different size classes of**  
720 ***Fractofusus* on the H14 surface.** SP refers to shared parents models, and LCM refers to  
721 linked cluster models.  $p_d = 1$  corresponds to a perfect fit of the model on the data, while  $p_d =$   
722 0 corresponds to no fit. The large size class was randomly distributed, but was approximated  
723 by a cluster model, which was required for input into Programita.<sup>9</sup>

724