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1 How do plankton species coexist in an apparently unstructured environment?

2
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13
14 **Key-words:** plankton paradox, niche theory, biodiversity, pelagic environment, principle of
15 competitive exclusion.

16 17 **Abstract**

18
19 In a paper entitled the paradox of plankton, Hutchinson asked "*how it is possible for a number of*
20 *species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts*
21 *of materials*". Particularly relevant for phytoplankton, this paradox was based on two implicit, and
22 perhaps naive, postulates, i.e. (i) that all plankton species have similar requirements and (ii) that the
23 marine environment is relatively homogeneous in space and time. A number of hypotheses, based on
24 purely theoretical or experimental studies, have been proposed to solve this conundrum, ranging from
25 spatio-temporal environmental heterogeneity to biotic chaotic variability. Here, we characterize the
26 ecological niche of 117 plankton species belonging to three different taxonomic groups and show that
27 all species have a niche sufficiently distinct to ensure coexistence in a structured marine environment.
28 We also provide evidence that pelagic habitats are, unsurprisingly, more diverse in space and time
29 than Hutchinson imagined, the marine environment being neither unstructured nor stable in space
30 and time. We therefore conclude that the niche theory, and its corollary the principle of competitive
31 exclusion, apply as much for the plankton as for other forms of life, be they terrestrial or marine.

32 33 **1. Introduction**

35 Marine plankton is composed of both uni- and multicellular organisms covering a wide range of size,
36 from less than 0.2 μm (virio plankton) to a few meters (e.g. the giant jellyfish *Nemopilema nomurai*)[1].
37 They are at the basis of the food web and play a key role in carbon dioxide regulation, influencing the
38 composition of the Earth's atmosphere [1–4]. The great diversity they exhibit has fascinated marine
39 biologists for a long time [5–7] and it is now apparent that there is even more diversity than originally
40 realised [8,9]. The mechanisms sustaining the plankton biodiversity remain debated, however, because
41 it is assumed that plankton species coexist in an apparently homogeneous environment with few
42 niches (*sensu* Hutchinson realised niche i.e. the set of environmental conditions modulated by biotic
43 interactions, enabling a species to grow and reproduce [10]) thought to be available [11,12].

44

45 Although it has been suggested that plankton species may share niches and coexist [13], many
46 theoretical and laboratory studies have tried to resolve the “paradox of the plankton”[11] and have
47 shown that the number of coexisting plankton species at equilibrium in a community cannot exceed
48 the number of limiting resources [14–17]. Consequently, coexistence of a large number of species on
49 a small number of limiting resources is only possible when other mechanisms are involved such as (i)
50 temporal heterogeneity (i.e. a continuously changing pelagic environment due to the seasonal changes
51 in hydro-meteorological forcing) and its influence on the structure of the water column [11,18–20], (ii)
52 spatial heterogeneity in the relative resource supply rate [21]), (iii) spatial subdivision [22], (iv) chaotic
53 variations in species abundance induced by competition [23] or (v) difference in the array of resources
54 limiting species growth [17,24]. The tenet that underlies the paradox of the plankton —that the
55 plankton environment is unstructured and so different plankton share the same niche, and therefore
56 the question of whether niche separation might promote plankton coexistence— has received little
57 attention, however.

58

59 In this article, we examine how niche separation can enable plankton coexistence. Niche separation,
60 which is often estimated by the degree of overlapping (i.e. the opposite of niche separation)[25],
61 results from the principle of competitive exclusion [26,27]. By allowing a better exploitation of the
62 available resources, this mechanism has been shown to enable terrestrial plant species coexistence
63 [28,29]. Here, we examine the two postulates on which the paradox of the plankton is based, i.e. (i) do
64 plankton species share niches and (ii) is the oceanic environment unstructured. To do so, we estimate
65 the degree of niche overlapping of 117 plankton species belonging to three taxonomic groups
66 (diatoms, dinoflagellates and calanoid copepods). We show that species' niches of the three taxonomic
67 groups are well separated and that the environment is much more structured in space and time than
68 Hutchinson envisioned [11]. We conclude that these two mechanisms jointly ensure plankton species
69 coexistence.

70

71 **2. Materials and Methods**

72

73 (a) Biological data

74

75 Plankton abundance data came from the Continuous Plankton Recorder (CPR) survey (Supplementary
76 Text S1)[30]. It is a long-term plankton monitoring programme using a high-speed plankton recorder
77 sampling at a depth of ~7-10m. Started in 1931, the CPR programme has since sampled plankton on a
78 monthly basis in the North Atlantic Ocean and its adjacent seas [31,32]. We used the data collected
79 between 1998 and 2018 in the North Atlantic Ocean and its adjacent seas [33]. This time period was
80 chosen because it corresponds to the period covered by the environmental datasets we used (see
81 Sections b and c). Species that were found in less than 100 CPR samples were removed from the
82 analysis so that the total number of species used was 117; this reflected abundance data for 71
83 phytoplankton (i.e. 45 diatoms and 26 dinoflagellates) and 46 calanoid copepod taxa.

84

85 (b) Environmental data

86

87 We used a set of nine different environmental variables to characterise the niches of the 117 species.
88 The chosen variables were: bathymetry (in m), nitrate, phosphate and silicate concentrations (mmol.m^{-3}),
89 Mixed Layer Depth (MLD, m), temperature ($^{\circ}\text{C}$), Photosynthetically Active Radiations (PAR, $\text{E.m}^{-2}.\text{day}^{-1}$),
90 salinity (no unit) and chlorophyll-a concentration (mg.m^{-3}). Detail descriptions and references
91 for each dataset are provided in Supplementary Text S2.

92

93 (c) Data pre-processing

94

95 We used the environmental data collected between 1998 and 2018 to work on a common time period
96 with respect to all datasets. All data were subsequently arranged on a grid covering the North Atlantic
97 Ocean (100°W - 10°E and 35°N - 65°N). By means of nearest-neighbour interpolation [34], we attributed
98 to each CPR sample a value for each of the nine chosen environmental variables at a depth of 8 m
99 (except for bathymetry), a value included in the range of sampling depth of the CPR instrument [30,31].
100 All the samples with a missing value along a single dimension were discarded prior to the analyses. We
101 therefore used a total of 90,527 CPR samples.

102

103 (d) Niche separation

104

105 To characterise and compare the multidimensional niches of the 117 planktonic species, we used the
106 recently proposed “species chromatogram” method [35,36]; this technique uses a chromatogram to
107 display the multidimensional niche of a species in a two-dimensional space. To do so, p-standardised
108 environmental gradients (one per environmental variable, e.g. temperature or nutrients), representing
109 the p-niche environmental dimensions, are defined between 0 (the lowest value taken by an
110 environmental variable) and 1 (the highest). Each gradient is divided into α equidistant categories (here
111 $\alpha=50$ for all chromatograms). For each category along each dimension (i.e. gradient), the mean species
112 abundance is estimated by averaging the values of the k% of the CPR samples (associated to that
113 category by means of the nearest-neighbour interpolation, see the previous section) with the highest
114 abundance values (here k= 5%), if at least m samples are present in that category (here m=20 CPR
115 samples). The mean abundances along each dimension are then standardised between 0 and 1, and
116 smoothed by means of a second-order simple moving average to alleviate the noise associated with
117 the CPR data. Finally, the niche is displayed as an array of coloured cells, which is called a species
118 chromatogram (Supplementary Figure S1-12)[36].

119

120 As each environmental gradient is globally standardised between 0 and 1, the niches of different
121 species can be compared and a degree of niche overlapping (called index D) can be estimated among
122 species [36]. This index is estimated by considering the categories with an abundance greater than or
123 equal to a threshold T along each dimension, with $0 < T \leq 1$. They are then used to calculate the niche
124 hypervolume, the shape of the niche being assimilated to a hyperrectangle. D is finally assessed for
125 each pair of species by calculating the ratio of the hypervolume of the niche common to the two
126 species on the total volume filled by the two species. The method is fully described in Kléparski &
127 Beaugrand [36].

128

129 Here, D was estimated for each pair of plankton species and for each combination of 1 to p-
130 environmental dimensions (i.e. 1 to p-dimensions considered simultaneously) and five thresholds T: 0,
131 0.1, 0.25, 0.5 and 0.75. For phytoplankton (i.e. diatoms and dinoflagellates), we chose eight
132 environmental dimensions (p=8): bathymetry, nitrate, phosphate and silicate concentrations, MLD,
133 temperature, PAR and salinity (Figure 1 and Supplementary Figure S1-8). For copepods, we used six
134 dimensions (p=6): bathymetry, MLD, temperature, PAR, salinity and chlorophyll-a concentration
135 (Figure 1 and Supplementary Figure S9-12). D was calculated among species belonging to the same
136 taxonomic group, i.e. among diatoms (45 species), dinoflagellates (26 species), phytoplankton (45
137 diatoms + 26 dinoflagellates = 71 species) or calanoid copepods (46 species).

138

139 All species chromatograms on which index D is based are displayed in Supplementary Figures S1-12.
140 We have synthesized the information of all species chromatograms by means of a community
141 chromatogram [35,36]. To do so, species' abundance was first replaced by 1 when its standardised
142 abundance was higher than or equal to 0.5 in a category [35](see Figure 1a-d). Then, we estimated the
143 number of co-occurring species in each category of the chromatogram and we converted it into
144 percentage. Therefore, a community chromatogram displays the percentage of co-occurring species in
145 each environmental category.

146

147 (e) Habitat diversity

148

149 Habitat diversity of the pelagic environment was estimated with respect to each environmental
150 variable (but bathymetry that is constant) by means of the Shannon entropy [37]. In other words, we
151 quantified the diversity of values that is taken by an environmental variable for each day or in each
152 geographical cell. To do so, eight environmental matrices (121 latitudes x 441 longitudes x 24 depth
153 levels (except for MLD) x 7670 days) were used and standardised between 0 (i.e. the lowest value of
154 an environmental variable at the scale of the North Atlantic) and 1 (i.e. the highest). The environmental
155 values taken by each matrix were then divided into 50 categories and the habitat diversity $H(S)$
156 (expressed in bit) was calculated as follows:

157

$$158 \quad H(S) = - \sum_{i=1}^{50} S_i \times \log_2(S_i) \quad (1)$$

159

160 With S_i the probability that the value of the i^{th} category was observed, i.e. its relative frequency. The
161 estimate of the Shannon entropy was performed in two ways for each year between 1998 and 2018:
162 (i) at a daily scale using all geographical cells and depth levels between 0 and 20 m and (ii) at a spatial
163 scale using all the days and depth levels between 0 and 20m. The resulting annual cycles were then
164 averaged (1998-2018).

165

166 **3. Results**

167

168 (a) Niche separation

169

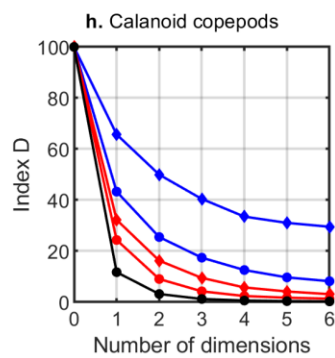
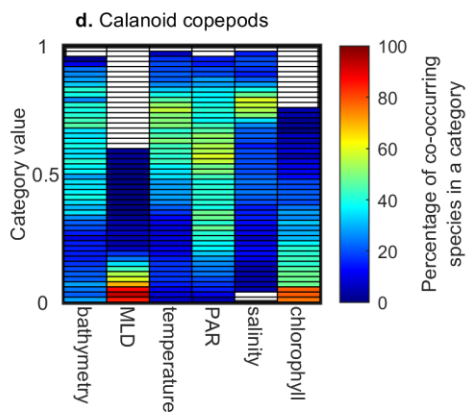
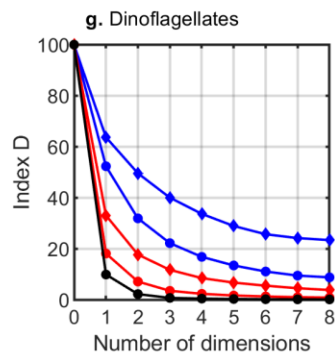
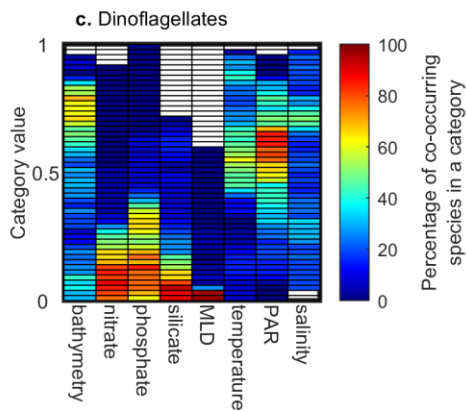
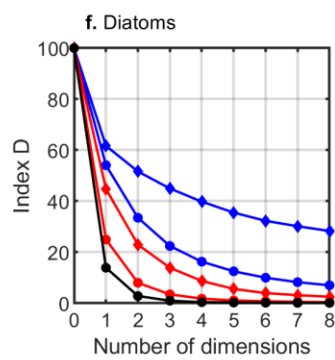
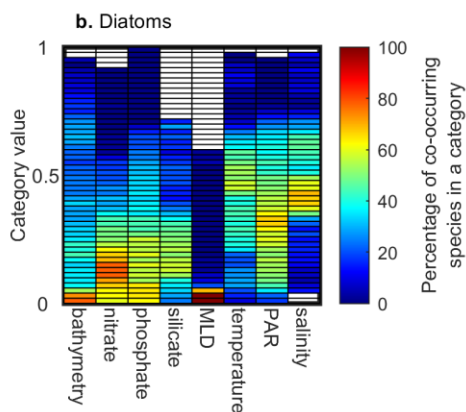
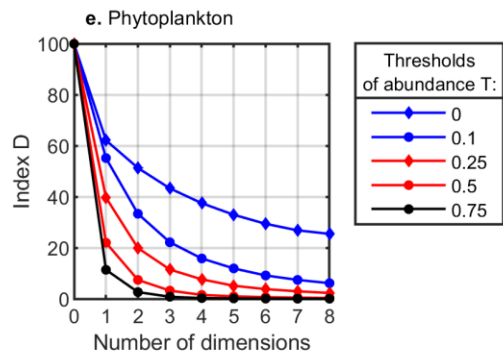
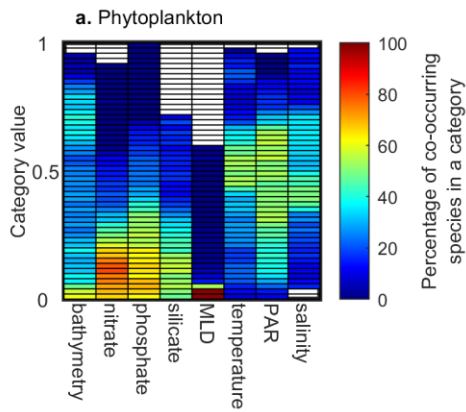
170 Species chromatograms are all displayed in Supplementary Figure S1-12. Their examination revealed
171 that each species has a unique chromatogram and therefore a specific niche, although many overlaps
172 were observed along all niche dimensions. The species chromatograms were summarised by
173 taxonomic group under the form of a community chromatogram, where species abundance was

174 replaced by the percentage of co-occurring species in an environmental category (Figure 1a-d). At this
175 organisational level, niche separation occurred between diatoms and dinoflagellates along five niche
176 dimensions (bathymetry, silicate, temperature, PAR and salinity; Figure 1b-c). Similarly, a clear niche
177 separation can be seen between phytoplankton and copepods with respect to salinity, although the
178 two groups have overlapping chromatograms for bathymetry, temperature and PAR (Figure 1a and d).
179 Hence, each group seems to have distinct environmental requirements, although niche overlaps are
180 the rule.

181

182 The calculation of the degree of niche overlapping (i.e. Index D) confirmed that species niches were
183 rapidly separated when the number of environmental dimensions of the niche rose (Figure 1e-h). Niche
184 overlapping diminished rapidly below 30% for the four taxonomic groups (Figure 1e-h). We therefore
185 investigated whether T (i.e. the threshold of abundance between 0 and 1) influenced our perception
186 of niche separation. When T increased from 0 to 0.75, overlapping rapidly reached a value below 20%
187 and even close to 0% when T becomes higher than 0.25. Consequently, the niches of the four groups
188 were almost totally separated towards the optimal part of their niche (i.e. the part of the niche where
189 a species has its highest abundance [38,39]), although some overlapping was still observed in the
190 suboptimal parts (i.e. the parts where a species has low abundance, i.e. when $T < 0.25$) (Figure 1e-h), as
191 might be the expected outcome of competition and natural selection [40].

192



194 **Figure 1. Community chromatograms and changes in the degree of niche overlapping for four groups of**
195 **plankton.** Community chromatogram of (a) phytoplankton, (b) diatoms, (c) dinoflagellates and (d) calanoid
196 copepods. In a-d each column represents an environmental dimension. The Y axis corresponds to the 50
197 environmental categories standardised between 0 and 1, i.e. it represents all the values taken by an
198 environmental variable from the lowest (bottom category) to the highest (top category). Colours denote the
199 percentage of co-occurring species in each category. High co-occurrence values are in red and low values in blue.
200 Categories where no CPR samples are available are shown in white. Panels e-f represent the changes in the
201 degree of niche overlapping for (e) phytoplankton, (f) diatoms, (g) dinoflagellates and (h) calanoid copepods.
202 Niche overlapping has been estimated by means of a species chromatogram (i.e. index D, M&M section).
203 Overlapping was assessed by considering simultaneously an increasing number of environmental dimensions,
204 from 1 to 8 for phytoplankton, diatoms and dinoflagellates, and from 1 to 6 for calanoid copepods. Overlapping
205 among species was based on five thresholds of abundance $T=0$ (blue lines with diamond), 0.1 (blue lines with
206 dot), 0.25 (red lines with diamond), 0.5 (red lines with dot) and 0.75 (black lines with dot).

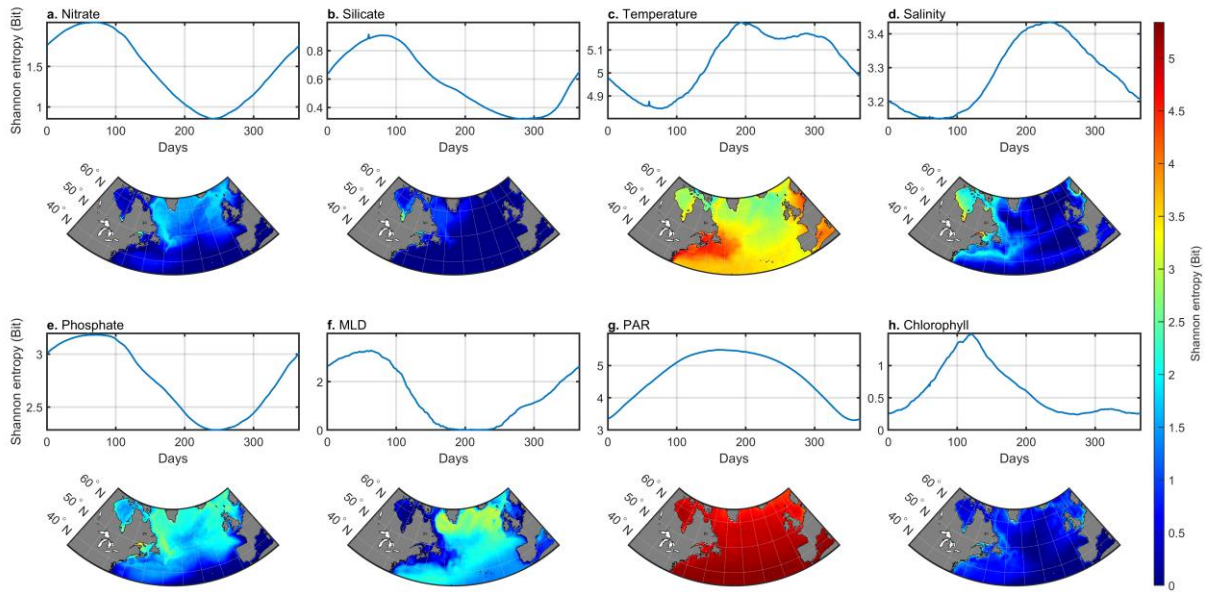
207

208 (b) Habitat diversity

209

210 We quantified habitat diversity in the North Atlantic Ocean by means of the Shannon entropy. The
211 analysis was performed in two ways. First, based on different depth levels (0-20 m) for all geographical
212 cells of the North Atlantic, we found two different daily patterns in habitat diversity: the first pattern
213 revealed higher diversity with respect to nutrients, MLD and chlorophyll-a in Spring (plots in Figure 2a,
214 b, e, f and h) and the second pattern revealed high diversity in Summer for temperature, salinity and
215 PAR (plots in Figure 2c, d and g). Second, based on depth levels (0-20m) and days, we identified spatial
216 patterns in habitat diversity. High diversity was found in the northern parts of the North Atlantic Ocean
217 for nutrients, MLD and chlorophyll-a (maps in Figure 2 a, b, e, f and h) whereas high habitat diversity
218 was found along continental shelves and in the southern part of the North Atlantic Ocean for
219 temperature and salinity (maps in Figure 2c-d). PAR showed high habitat diversity everywhere in the
220 North Atlantic (Figure 2g). Our results therefore confirm that not only the environment is diverse in
221 space and time but that it is also highly impermanent at the same scales (Figure 2).

222



223
 224 **Figure 2. Habitat diversity in the North Atlantic Ocean.** Habitat diversity for (a) nitrate, (b) silicate, (c)
 225 temperature, (d) salinity, (e) phosphate, (f) MLD, (g) PAR and (h) chlorophyll-a. Changes in temporal diversity are
 226 shown by the plots and changes in spatial diversity by the maps below the plots. Habitat diversity was assessed
 227 by means of the Shannon entropy estimated on the annual changes of each environmental variable (see M&M
 228 section). High values of Shannon entropy (red colour in the maps) mean that habitats diversity is high and low
 229 values (blue colour in the maps) that habitat diversity is small.

230
 231 **4. Discussion**

232
 233 It is known that diatoms and dinoflagellates have distinct environmental requirements [41]. Here, our
 234 results are going farther and show that the niches of both phyto and zooplankton species rapidly
 235 separate when the number of niche dimensions rises (Figure 1). They also demonstrate that the pelagic
 236 environment is not only diverse but also impermanent in space and time (Figure 2), a result that has
 237 been shown by many studies since the original paper of Hutchinson [42–44]. Therefore, the two
 238 implicit postulates on which the Hutchinson’s paradox was based are incorrect. High niche
 239 differentiation leads species to have a unique combination of environmental conditions (i.e. a unique
 240 niche) where their performances in terms of growth and reproduction are optimal [28]. Therefore,
 241 each species covers a part of the multidimensional environmental space and the segregation along
 242 various environmental niche dimensions enables them to coexist in space and time, a mechanism that
 243 has been suggested to enable terrestrial plant coexistence [28,29]. Furthermore, we have shown that
 244 niche separation can occur along a single unique dimension in a multivariable space. For example, two
 245 phytoplankton species may still coexist if they share the same niche for a nutrient but utilise a different

246 light wavelengths [45]. In other words, to simply resolve the plankton paradox we just need to fully
247 understand marine environmental heterogeneity as it applies to the plankton.

248
249 Because of the duality between the niche space and the real physical space (i.e. Hutchinson's duality
250 [46]), niche separation (Figure 1) can be related with the diversity of habitats we have observed (Figure
251 2). Environmental variability is an important mechanism known to promote species coexistence
252 because of a mechanism known as the "storage effect" [47,48]. This mechanism has three
253 requirements: (i) the species of a given community have to develop strategies to survive during
254 unfavourable environmental conditions, (ii) these species have distinct responses to environmental
255 variability (i.e. distinct niches) and (iii) this variability affects competition, meaning that the niche-
256 environment interaction modulates competition (i.e. a species is more resistant to competition when
257 its environment is more in adequation with its niche and inversely)[49,50].

258
259 Expectedly, niche separation is maximal at the optimal part of a species' niche (Figure 1e-h). Therefore,
260 this separation alleviates competition and prevents competitive exclusion. Niche separation takes
261 place through evolution via an alteration in life history strategies. Plankton have developed various
262 strategies, like the development of pigments, cysts, spores, resting eggs or lipidic bags, that enable
263 them to survive during adverse environmental conditions [51–55]. Some strategies (e.g. diatom
264 morphological traits) even explain phenology and annual plankton succession [56,57]. Our study
265 therefore shows that the niche theory, and its corollary the principle of competitive exclusion, applies
266 for the plankton as for other groups, be they terrestrial or marine.

267

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388

389 **Data availability**

390

391 All the data used in this article are already freely available (see the M&M section and Supplementary
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393

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399

400 **Conflict of interest**

401

402 The authors declare no conflict of interest.