

# 1 **Biodiversity trends are stronger in marine than terrestrial assemblages**

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30 **Summary**

31 Human activities have fundamentally altered biodiversity. Extinction rates are  
32 elevated and model projections suggest drastic biodiversity declines. Yet, observed  
33 temporal trends in recent decades are highly variable, despite consistent change in  
34 species composition. Here, we uncover clear spatial patterns within this variation. We  
35 estimated trends in the richness and composition of assemblages in over 50,000 time-  
36 series, to provide the most comprehensive assessment of temporal change in  
37 biodiversity across the planet to date. The strongest, most consistent pattern shows  
38 compositional change dominated by species turnover, with marine taxa experiencing  
39 up to fourfold the variation in rates of change of terrestrial taxa. Richness change  
40 ranged from no change to richness gains or losses of ~10% per year, with tropical  
41 marine biomes experiencing the most extreme changes. Earth is undergoing a process  
42 of spatial reorganisation of species and, while few areas are unaffected, biodiversity  
43 change is consistently strongest in the oceans.

44 **Main Text**

45 Biodiversity is changing rapidly throughout the Anthropocene. Against a background  
46 of elevated extinction rates<sup>1,2</sup>, local biodiversity change results from multiple  
47 interacting drivers that influence the abundance and distribution of species. Different  
48 regions of the globe are projected to experience different trends in biodiversity  
49 change, particularly due to variation in the strength of drivers such as land use  
50 intensity<sup>3</sup> and climate change<sup>4</sup>. There are widespread changes in the identities of  
51 species that live in any one location (species composition), whereas shifts in the  
52 numbers of species (species richness) show a mixed pattern with increasing,  
53 decreasing, or static trends<sup>5-8</sup>. However, the spatial distribution of the locations most

54 affected is unknown. Here, we map biodiversity change, as species richness and  
55 composition, to establish whether there are systematic trends in the biogeography of  
56 biodiversity change. Our analysis compares marine and terrestrial realms, as well as  
57 different biomes, and latitudinal bands examined as polar, temperate, and tropical  
58 regions of the globe.

59

60 Biodiversity and its change is unevenly distributed on the planet<sup>9,10</sup>, and unevenly  
61 sampled<sup>11-14</sup>. Detecting geographic variation in biodiversity trends will inform  
62 conservation prioritisation and improve estimates of global biodiversity change.  
63 Moreover, quantifying this spatial distribution will help refine hypotheses about the  
64 drivers of biodiversity change. The spatial distribution of drivers of biodiversity  
65 change is heterogeneous<sup>15,16</sup> and fundamentally differs between the marine and  
66 terrestrial realms<sup>17</sup>. Specifically, there is more spatial overlap between climate change  
67 and other drivers of change in the marine realm than in the terrestrial realm<sup>17</sup>.  
68 Understanding the biogeography of biodiversity change across realms is essential for  
69 reliable forecasting future change and its consequences.

70

71 Quantifying biogeographic patterns of biodiversity change will allow us to assess the  
72 ongoing spatial re-organisation of species. This reorganisation is being driven by  
73 climate change driven range shifts<sup>4,18</sup>, altered species abundance due to land-use  
74 change<sup>3</sup> and widespread species introductions<sup>19</sup>. Local or regional richness will  
75 decline when species losses exceed species gains, for example, in areas where land-  
76 use intensity is high<sup>3</sup> and/or when range sizes contract<sup>20</sup>. Conversely, local or regional  
77 richness will increase when species gains exceed losses, occurring, for example, in  
78 places where species are introduced<sup>21-23</sup> and where ranges expand<sup>24,25</sup>, or when

79 species are favoured by land-use change<sup>26</sup>. Combinations of different anthropogenic  
80 drivers can lead to increases or decreases, depending on the magnitude of each  
81 driver<sup>27</sup>.

82

83 Here, we quantified biogeographic variation in patterns of change in both species  
84 richness and composition from a compilation of over 50,000 local assemblage time  
85 series (ranging from 2 to 97 years; mean = 5.5 years) across the globe. We use the  
86 BioTIME database, which is currently the largest collation of assemblage time series  
87 (332 studies analysed<sup>28</sup>; plus 26 other studies; see Table S1 in Dornelas et al. 2018;  
88 Extended Data Fig. 1). The null expectation is that overall species richness should  
89 remain largely stable even when compositional turnover is high, due to species gains  
90 and losses at local scales being approximately balanced and widespread community  
91 regulation<sup>29-31</sup>. Results from a number of analyses are consistent with this  
92 expectation<sup>5-8,29</sup>. Yet there is scope for non-random spatial patterns within the  
93 distribution of local species gains, losses and compositional change. Here, we  
94 quantify variation in biodiversity change trends among realms, biomes, latitudinal  
95 bands and taxa.

96

### 97 **Biodiversity trends across the globe**

98 To examine biogeographical patterns in biodiversity change we estimated trends in  
99 richness and composition change using hierarchical linear models. After standardising  
100 for spatial extent and sampling effort of each time-series, we quantified biogeographic  
101 variation by examining departures from overall trends for 48 biomes and 9  
102 taxonomic-habitat groupings (hereafter referred to as *taxa*; amphibians, benthos,  
103 birds, fish, invertebrates, mammals, marine invertebrates/plants, plants, and multiple

104 taxa) that were nested within biomes (resulting in 105 biome-taxa combinations [table  
105 S1]). We also examined the robustness of our biome-taxa models by fitting a second  
106 set of simpler hierarchical models, where taxonomic groups were nested within  
107 latitudinal bands (i.e., polar, temperate, tropical) for each realm (marine, terrestrial,  
108 freshwater; [table S2] *see supporting information for details*).

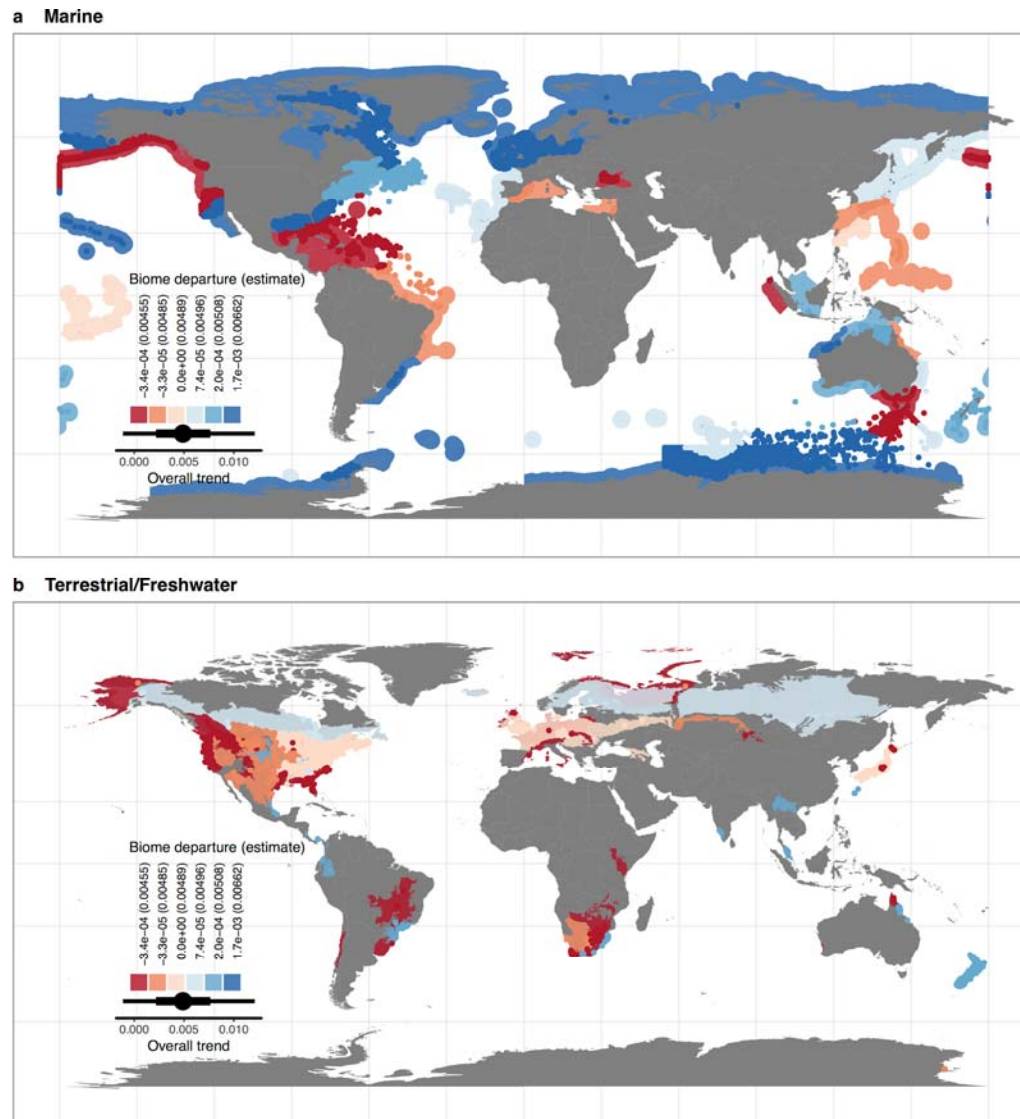
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110 Our results show that variation in biodiversity change is greater in the marine versus  
111 the terrestrial and freshwater realms. The overall trend in richness change was not  
112 statistically distinguishable from zero (Fig. 1), neither globally, nor at the biome level.  
113 This result was robust to sensitivity analyses regarding time series duration and start  
114 year (Extended Data Figs. 4 to 7). However, variation in departures from the overall  
115 trend were almost four times greater among marine biomes (median biome departure  
116 range: -0.0014 -- 0.0017,  $n = 33$ ; Fig. 1a) compared with terrestrial and freshwater  
117 biomes (-0.0006 -- 0.0002,  $n = 15$ ; Fig. 1b). Thus, taxa in marine biomes frequently  
118 represented extremes at both ends of the range of observed change in species richness  
119 - negative trends of approximately 10% species loss per year and positive trends  
120 approaching 15% species gains per year (Fig. 2a). At the taxa-level, this volatility in  
121 marine species richness change meant that a higher proportion of biome-taxa  
122 combinations were undergoing richness changes that differed from zero with 95%  
123 probability (36/78) compared with terrestrial and freshwater taxa (7/27).

124

125 Richness trends varied substantially across taxa within biomes, and this variation was  
126 spatially structured, with the most pronounced trends found within tropical latitudes.  
127 Negative richness trends (i.e. slope estimates with 90% credible intervals that do not  
128 include zero) were present for taxa in five out of twelve marine tropical biomes, with

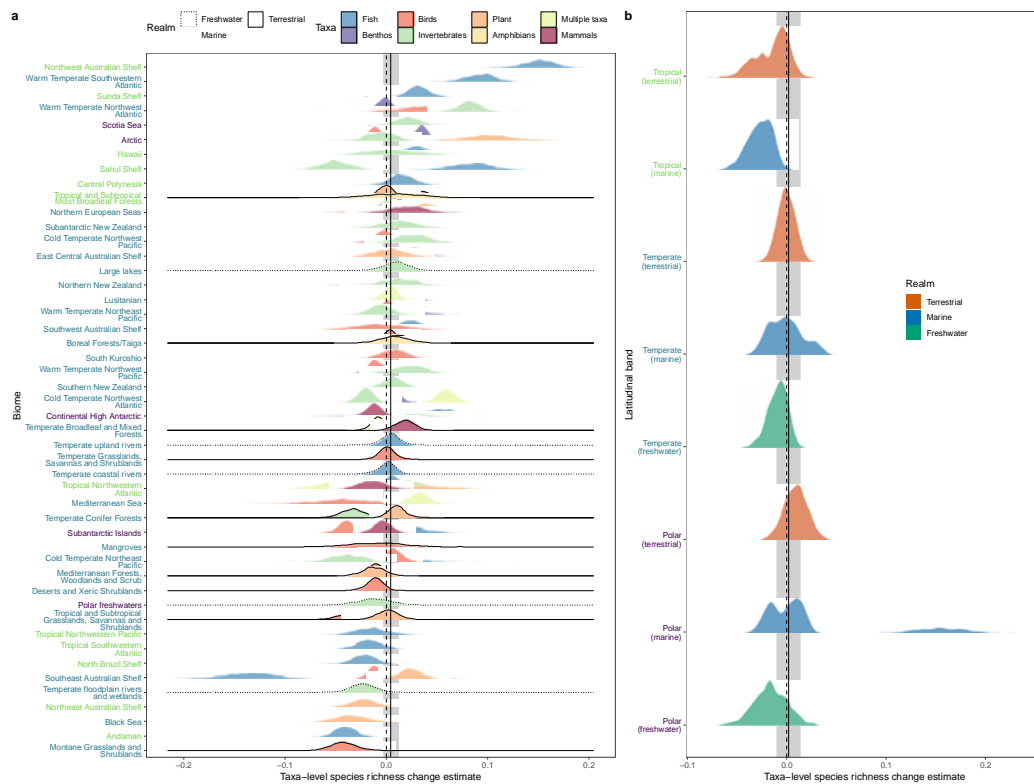
129 positive trends present in three (Fig. 2a). These results were consistent with our  
130 simpler hierarchical model that showed overall declines within tropical latitudes for  
131 marine taxa (Fig. 2b). Locations where species losses outweigh gains could be driven  
132 by range contractions, or by the loss of more specialised or thermally restricted  
133 species as climate change, land use or seascape change, and other anthropogenic  
134 drivers affect tropical habitats<sup>32,33</sup>. Geographic gaps from terrestrial tropical systems  
135 remain in our assemblage time series data, precluding direct comparison between the  
136 realms (see also Extended Data Fig. 1). The high rates of change we observed in the  
137 marine tropics are consistent with predictions that tropical species will be relatively  
138 sensitive to extreme heat events, because they are closer to their physiological limits,  
139 resulting in biodiversity loss<sup>34</sup>. However, overexploitation, pollution, and other threats  
140 are likely also contributing to biodiversity change.  
141



142

143 **Figure 1.** The overall trend in assemblage species richness change across biomes in the marine and  
144 terrestrial realm does not differ from zero; bar depicts 50% (thick) and 90% (thin) credible intervals.  
145 Shading represents positive (blue) and negative (red) departures from the overall trend (0.005) for each  
146 biome; numbers in legend denote the departure and the biome-level (overall + departure) estimate in  
147 brackets. 90% credible intervals for all biome level estimates overlap zero. **a**, Marine biomes ( $n = 33$ )  
148 show both positive and negative departures from the overall trend, with more negative departures in the  
149 tropics, whereas there are no latitudinal trends in **b**, Terrestrial ( $n = 10$ ) and freshwater ( $n = 5$ ) biomes.  
150 Marine biomes show stronger variation in richness outcomes; particularly visible in the dark blue  
151 coastal polar regions and the cluster of dark red biomes in the Caribbean and southeast coast of  
152 Australia.

153



154

155 **Figure 2:** The magnitude of species richness change is more variable among taxa in marine biomes  
 156 than taxa in terrestrial or freshwater biomes. The overall trend in assemblage richness change (solid  
 157 vertical bar) does not differ from zero (grey shading depicts the 90% credible interval) for both **a**, the  
 158 biome-taxa model, and **b**, the simpler realm-climate-taxa model. Density ridges in **a** represent the  
 159 posterior distribution for the slope coefficients of each taxa-level coefficient (within each a biome); line  
 160 type and fill refer to the realm and taxon, respectively. Colour of biome label denotes latitudinal band  
 161 (light green tropical, blue green temperate and purple polar as shown in **b**). Density ridges in **b**  
 162 represent the posterior distributions of the slope coefficients for all taxa within a given combination of  
 163 realm and latitudinal band (climate) estimated with the realm-climate-taxa model.

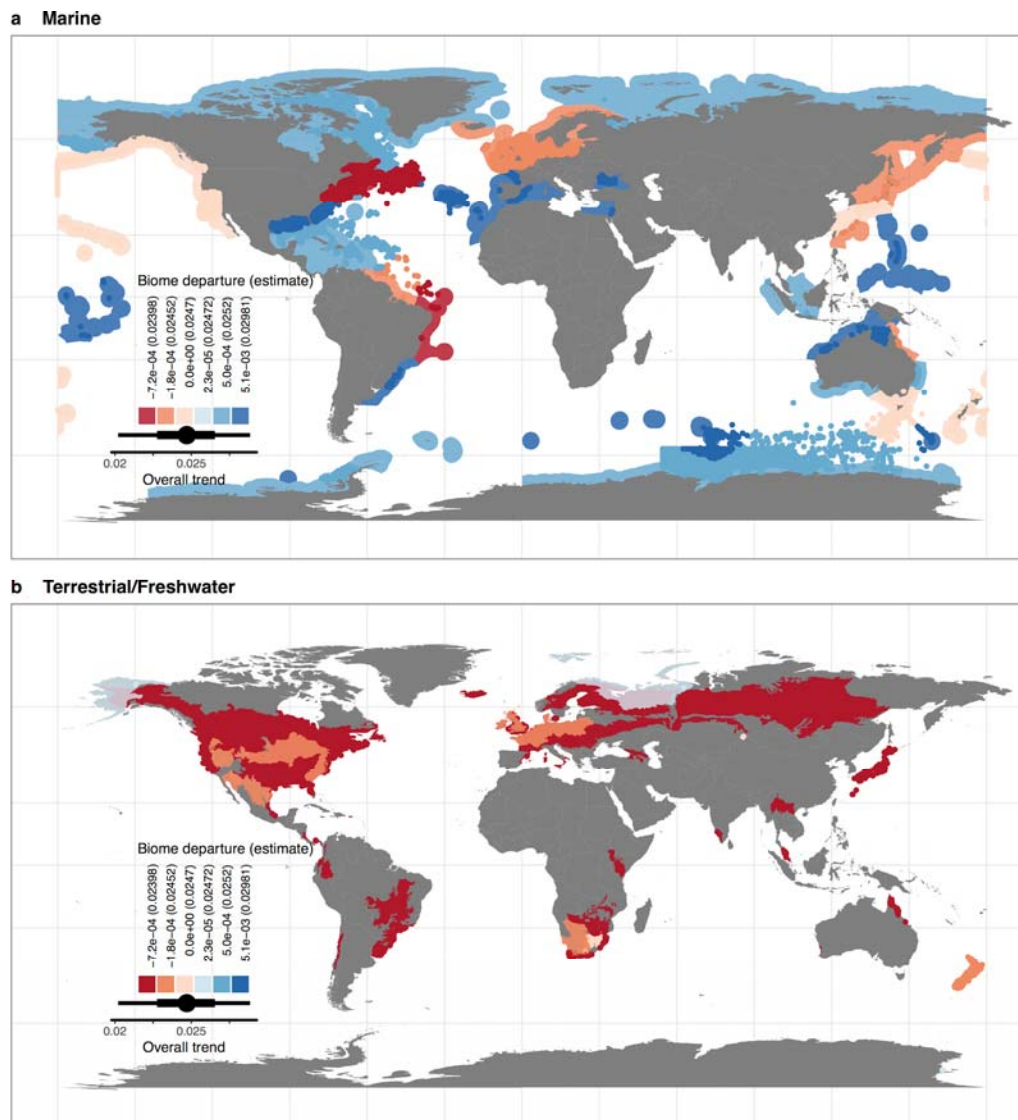
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166 To examine changes in species composition, we partitioned total Jaccard dissimilarity,  
167 calculated as the dissimilarity between the initial and each subsequent year of a time  
168 series, into the additive components of turnover and nestedness<sup>35</sup>. These trends  
169 describe directional compositional change relative to the initial assemblage, and the  
170 decomposition examines whether changes in community composition were due to the  
171 original species in assemblages being replaced by new species (turnover), or if  
172 assemblages were becoming smaller subsets of themselves or growing to include new  
173 species alongside the original species (nestedness). Overall, we found rates of  
174 *turnover* were positive and much greater (0.025; 90% credible interval: 0.021-0.029;  
175 Fig. 3) than the rate of change in *nestedness* (0.005; 0.004-0.006; Extended Data Fig.  
176 2). This means that compositional change was dominated by species replacement  
177 within assemblages, with approximately 25% of species within assemblages being  
178 replaced per decade. Marine biomes showed both positive and negative departures  
179 from the overall trend (i.e., depending on the biome, more and less compositional  
180 change over time than the global average; Fig. 3a). In contrast, the terrestrial biomes  
181 showed mostly negative departures from the global average (Fig. 3b), often in highly  
182 developed regions of the globe (e.g., Northeast US, Europe, Japan). Similar to our  
183 finding for species richness change, variation in rates of turnover were more than 1.5  
184 times greater in marine biomes (Fig. 3) and 2.5 times greater among marine taxa when  
185 compared to their terrestrial and freshwater counterparts (Fig. 4). Taxa in terrestrial  
186 and freshwater biomes represented 9 of the 10 lowest rates of turnover, whereas, 9 of  
187 the 10 highest rates of turnover were marine taxa (Fig. 4a). Fish in marine tropical  
188 biomes represented both ends of the spectrum, from among the lowest turnover rates  
189 (Tropical Southwestern Atlantic) to the highest observed turnover rate (Northwest  
190 Australian Shelf).

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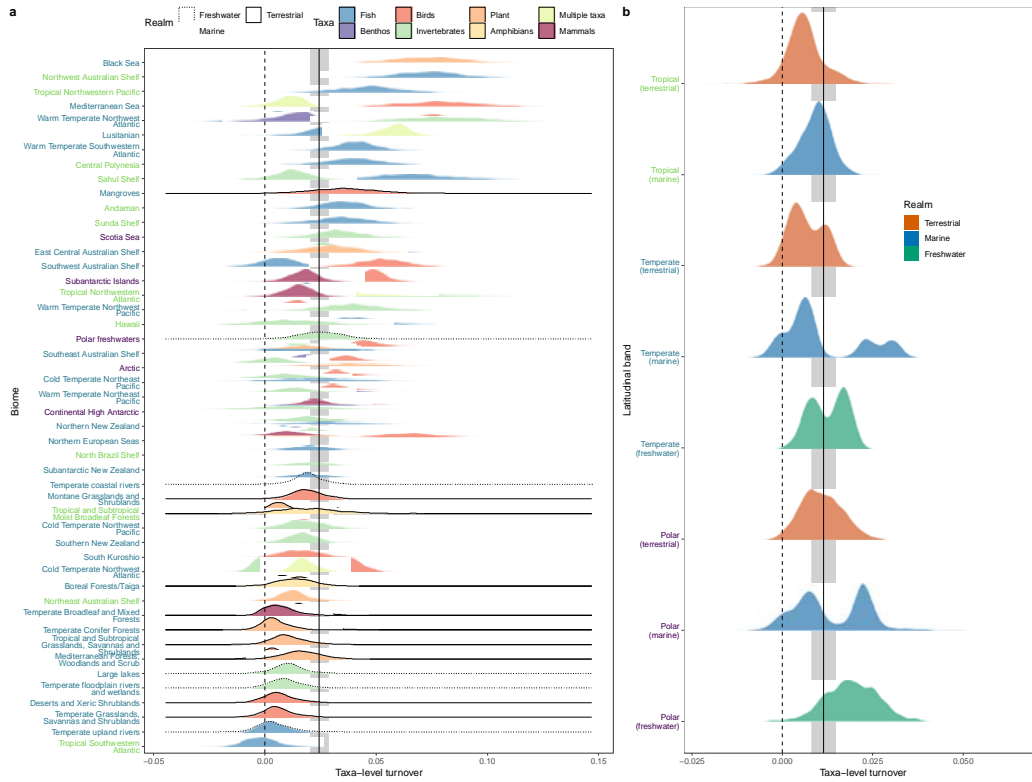
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193 **Figure 3.** Assemblages across the globe are experiencing high rates of species replacement (turnover  
194 component of Jaccard dissimilarity). **a**, Rates of new species replacing original species have both  
195 positive and negative departures from the overall trend in marine biomes, whereas **b**, terrestrial and  
196 freshwater biomes have mostly slower rates of turnover than the overall trend (red shading). Numbers  
197 in legend denote the departure and the biome-level (overall + departure) estimate in brackets.

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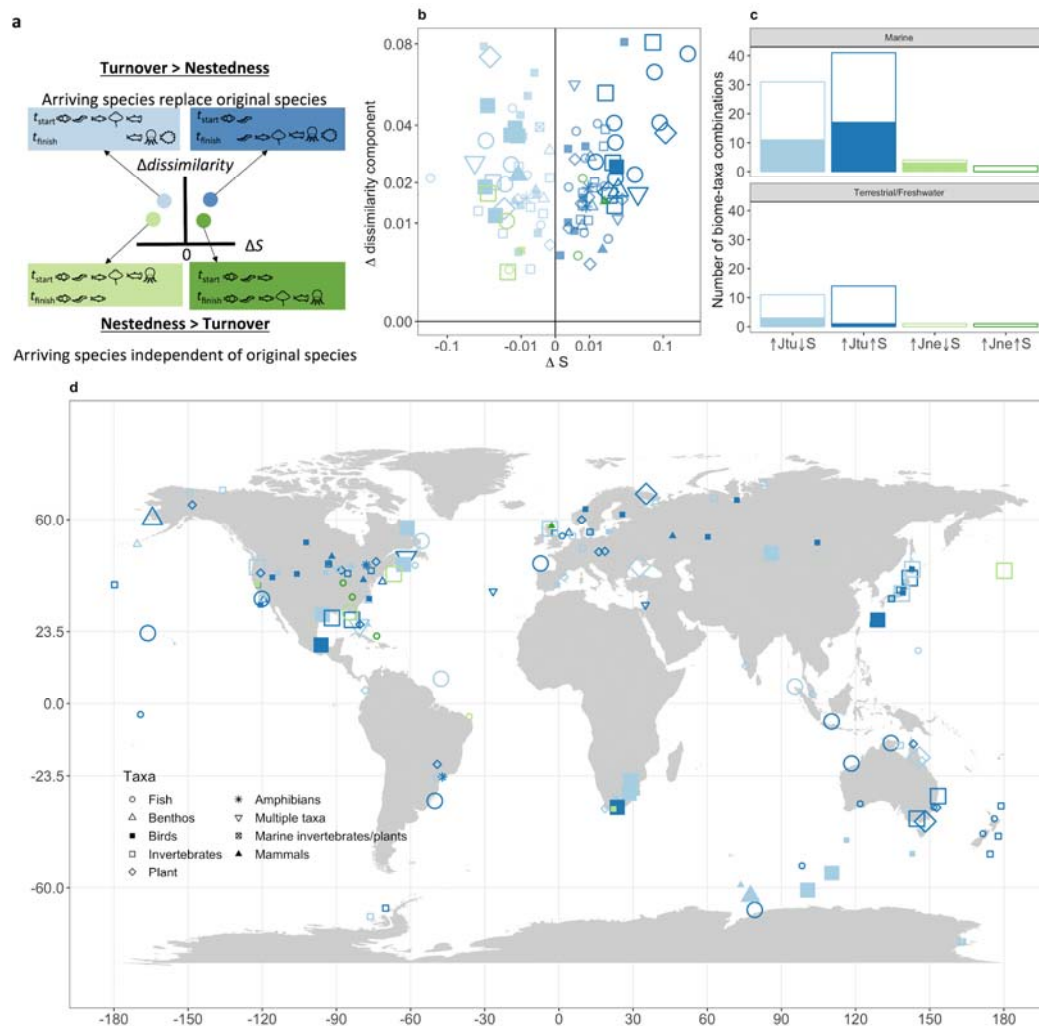
**Figure 4.** The magnitude and total variation of composition change (represented by the turnover component of Jaccard dissimilarity) is greater among taxa in marine biomes compared to taxa in terrestrial or freshwater biomes. The overall trend in turnover change per year is greater than zero (solid black line; grey shading depicts the 90% credible interval) for both **a**, the biome-taxa model, and **b** the simpler realm-climate-taxa model. Density ridges in **a** represent the posterior distribution for each taxa-level slope coefficient (within each a biome); linetype and fill refer to the realm and taxon, respectively. Colour of biome label denotes latitudinal band (light green tropical, blue green temperate and purple polar as shown in **b**). Density ridges in **b** represent the posterior distributions of the slope coefficients for all taxa within a given combination of realm and latitudinal band (climate) estimated with the realm-climate-taxa model.

214 **Linking richness and composition change**

215 To illustrate the relationship between trends in species richness and composition, we  
216 plotted the dominant component of composition change (turnover or nestedness) for  
217 each biome-taxa combination as a function of species richness change (Fig. 5a, b).  
218 When turnover is the dominant component, this relationship shows how fast new  
219 species are replacing original species, and whether or not these arrivals influence the  
220 total number of species in assemblages. We found rates of turnover change to exceed  
221 nestedness for more than 90% of biome-taxa combinations (97/105; Fig. 5b, c, d). For  
222 these taxa, approximately one-third (31/97) had both rates of turnover and species  
223 richness trends different from zero (Fig. 5c), with a balanced distribution of 14 cases  
224 of species richness losses, and 17 with gains. When nestedness is the dominant  
225 component, this relationship shows how fast assemblages are changing to become  
226 smaller subsets of the species initially observed. Among the eight biome-taxa  
227 combinations where nestedness exceeded turnover change (8/105; Fig. 5b, c, d), three  
228 marine taxa had increasing nestedness and detectable species richness losses. Spatial  
229 patterns of biodiversity change were highly heterogeneous (Fig. 5d), with locations in  
230 close proximity experiencing distinct trends in composition and richness change. For  
231 example, within the cold temperate northwest Atlantic marine biome (Fig. 5d,  
232 Extended Data Figure 3; encompassing the Gulf of Maine, Gulf of St. Lawrence, and  
233 south Newfoundland), the trend for invertebrate assemblages to become a smaller  
234 subset of themselves was in close proximity to five other groupings of taxa where  
235 turnover was the dominant component of composition change (benthos, birds, fish,  
236 marine invertebrates/plants and multiple taxa), among which there were trends for  
237 both species losses (e.g. birds) and gains (e.g. multiple taxa).

238

239



240

241 **Figure 5.** Conceptual and empirical relationships between changes in species richness and  
 242 composition. **a**, Conceptual model relating the turnover and nestedness components of species  
 243 composition change ( $\Delta$  dissimilarity) to changes in species richness ( $\Delta S$ ). When the turnover  
 244 component is larger than the nestedness component, new species entering assemblages replace the  
 245 original species (blue shaded boxes). Conversely, when the nestedness component is larger than the  
 246 turnover component, some original species of the assemblage remain, and the numbers of new species  
 247 entering the assemblage are largely independent of the original species (green shaded boxes). The  
 248 change in species richness documents the net change in the numbers of species in the assemblage (and  
 249 ignores their identity as either original or new species). **b**, Scatterplot showing the dissimilarity trend as  
 250 a function of the species richness trend. Each point represents a taxa-level group (shapes denoted in

251 panel **d** legend), and larger points indicate that both composition and richness trends differed from zero  
252 with 95% probability; CIs not shown and axes transformed for clarity. **c**, The number of taxa for each  
253 combination of change in species richness and species composition (measured as either the turnover,  
254 Jtu, or nestedness, Jne, component of Jaccard dissimilarity). Filled sections of each bar represent taxa  
255 where both species richness (*S*) and composition change (Jtu or Jne) differ from zero. **d**, Map showing  
256 the location of each biome-taxa combination. Point colours and sizes follow from panel **b**.  
257  
258

259 **Discussion**

260 Compositional change dominated by species turnover is the most striking and most  
261 prevalent pattern in biodiversity patterns across the globe. For the majority of taxa in  
262 biomes across the planet for which we have data, there was considerable replacement  
263 of species through time with no associated species richness changes. The consistent  
264 pattern of species replacement is likely underpinned by a diverse suite of drivers.  
265 Such reorganization is consistent with regulatory mechanisms for species richness.  
266 Community regulation in species richness is widespread<sup>30</sup>, and may be driven by  
267 shared resource availability<sup>29</sup> or by the continuous replacement of transient  
268 species<sup>36,37</sup>. Contemporary pressures such as introduced species<sup>21-23</sup>, replacement of  
269 localised specialists by widespread generalists, or range shifts in response to  
270 environmental change<sup>18,38,39</sup> may also help explain our finding of widespread  
271 composition change and variable richness change with an overall trend not  
272 distinguishable from zero.

273

274 Rates of species richness change and turnover were higher and more variable in the  
275 marine realm. Detecting this difference between realms generates hypotheses about  
276 the differences among realms in both drivers of biodiversity change and biotic  
277 responses to these drivers. The spatial distributions of anthropogenic drivers of  
278 change differ among realms<sup>17</sup> and different driver combinations have different effects  
279 on biodiversity change<sup>27</sup>. In addition, marine organisms may be more likely to  
280 respond to some drivers such as climate change<sup>34</sup> and marine assemblages may be  
281 able to turnover more rapidly due to higher connectivity in the marine realm<sup>40</sup>.

282

283 Amid widespread variation in biodiversity trends, we detect a signal of tropical  
284 marine regions having a distribution of trends more skewed towards richness  
285 extremes and high turnover. Particularly concerning are the two tropical marine  
286 biomes that show both negative trends in species richness and higher than average  
287 turnover of fish assemblages: Andaman and Tropical Northwestern Pacific. The  
288 tropics, which harbour the majority of the planet's biological diversity, are generally  
289 considered to be the most threatened regions of the planet<sup>41</sup>. Moreover, in the context  
290 of climate change, there are likely fewer species available to replace species lost in  
291 tropical zones that have entered no-analog warm temperature conditions<sup>42,43</sup>. If these  
292 trends are maintained, this pattern could lead to dramatic global losses of biodiversity  
293 and to the attenuation of the latitudinal diversity gradient, significantly altering the  
294 planet's biogeography.

295

296 Here, we identify hotspots of biodiversity change: key areas that represent increasing  
297 and decreasing extremes for biodiversity trends. In addition to the marine tropics,  
298 areas like Tasmania, Alaska, and the South of South Africa stand out as regions  
299 experiencing stronger negative biodiversity change. In contrast, the North Sea and  
300 Eastern North America emerge as areas experiencing increases in biodiversity change.  
301 This spatial and taxonomic variation in biodiversity trends means that global trends of  
302 biodiversity need to be based on spatially representative data. However, and despite  
303 using the largest compilation of biodiversity time series to date, our analysis suffers  
304 from many blind-spots. Our results highlight how improving our understanding of  
305 biodiversity change will require filling the gaps by improving biodiversity monitoring  
306 and moving towards global stratified random sampling of biodiversity.

307



308 In summary, biodiversity change has strong biogeographic variation. We have  
309 identified hotspots of richness gains and losses, as well as species replacement. The  
310 marine realm emerges as having the strongest change, and the marine tropics in  
311 particular, as having a higher prevalence of richness losses. This spatial variation  
312 suggests we need to abandon a view of homogenous loss of biodiversity, as the mean  
313 of local change across the globe does not differ from zero, and is not necessarily  
314 representative of local trends. Our work suggests an urgent need to better understand  
315 *why* there is such geographic variation. The spatial variation described here should  
316 inform conservation prioritisation by identifying the parts of the planet changing most  
317 rapidly, as well as those that are more stable. In the field of climate science, there was  
318 a shift in wording from global warming to climate change. Similarly, our results  
319 justify a shift in focus towards recognising that biodiversity change in the  
320 Anthropocene has contrasting effects in different parts of the planet.

## 321 **Methods**

### 322 **Data description and pre-processing**

323 The BioTIME database represents the largest global effort mobilizing assemblage  
324 time series (range = 2 to 97 years; mean = 5.5 years), includes 386 studies, and  
325 currently holds over 12 million records of abundance for over 45 thousand species  
326 across plants, invertebrates, fish, birds and mammals<sup>28</sup>. Analyses presented in this  
327 study are based on time series of abundance data (i.e., the studies that recorded counts  
328 of the number of individuals for each species in an assemblage).

329

330 As we were interested in quantifying biodiversity change at the local scale, studies  
331 with multiple sampling locations and extents greater than 71.7 km<sup>2</sup> were partitioned

332 into 96 km<sup>2</sup> grid cells (studies with extents < 71.7 km<sup>2</sup> were assigned to the grid cell  
333 in which they were centered). Each cell was given a unique identifier that was the  
334 concatenation of the study ID and the cell reference number. Species were then  
335 collated within each grid cell for each year, resulting in new assemblage time series  
336 within grid cells. For all assemblages in every cell and every year, we calculated the  
337 coverage of the sample, which is a measure of sample completeness<sup>44</sup> (mean = 0.95,  
338 sd = 0.11), and removed all assemblage-cell-year combinations with coverage less  
339 0.85 (meaning that for the time series retained, there was a <15% chance of another  
340 individual sampled being a new species).

341

342 Finally, we applied sample-based rarefaction to the minimum number of samples per  
343 year for each time series. We calculated community dissimilarity using pairwise  
344 Jaccard dissimilarity and the first year as the baseline, and species richness for each  
345 year of the time series. We also calculated the turnover and nestedness components of  
346 Jaccard dissimilarity to assess if the changes in compositional diversity were driven  
347 by species replacement or changes in species richness<sup>35,45</sup>.

348

### 349 **Models of biodiversity change**

350 We quantified biodiversity change using two complementary hierarchical models.  
351 Both models included the time series of assemblage dynamics within individual cells  
352 at the lowest level of the model, but differed in the way that these individual time  
353 series were grouped hierarchically. The biome-taxa (BT) model nested time series  
354 within ecological biomes ([http://maps.tnc.org/gis\\_data.html](http://maps.tnc.org/gis_data.html)<sup>46-49</sup>) and groups of taxa.  
355 The realm-climate-taxa (RCT) model nested time series within a grouping covariate  
356 that was the concatenation of realm (marine, terrestrial or freshwater), climate

357 (latitudinal bands denoting polar regions, temperate regions and the tropics) and taxa.  
358 The groupings of taxa for both models were based on the metadata of BioTIME, and  
359 included: amphibians, benthos, birds, fish, invertebrates, mammals, marine  
360 plants/invertebrates, plants, and multiple taxa for studies that measured more than one  
361 taxa group. We fit models where there were more than three cell-level times series per  
362 group, and discuss trends at the biome and taxa levels for the BT model, and for the  
363 realm-climate-taxa level for the RCT model, as the analytic technique is not well  
364 suited to describing trends at the cell-level where the data are sparse. Both models  
365 were fit with year as a population (or global) parameter, and year (i.e., the slope  
366 parameter) and the intercept were allowed to vary for each of the hierarchical levels of  
367 the models.

368

369 We quantified change in species richness and community composition (total Jaccard  
370 dissimilarity, and the turnover and nestedness components). Species richness was  
371 modelled assuming a Poisson error distribution and a log link function. This resulted  
372 in the BT model having the form:

373

$$\log(\mu_{k,j,i,t}) = \beta_0 + \beta_{0k} + \beta_{0k,j} + \beta_{0k,j,i} + (\beta_1 + \beta_{1k} + \beta_{1k,j} + \beta_{1k,j,i})x_{k,j,i,t},$$

374

$$y_{k,j,i,t} \sim \text{poisson}(\mu_{k,j,i,t}),$$

375

376 where  $x_{k,j,i,t}$  is the time in years,  $\beta_0$  and  $\beta_1$  are the global intercept and slope (often  
377 termed fixed effects),  $\beta_{0k}$  and  $\beta_{1k}$  are the biome-level departures from  $\beta_0$  and  $\beta_1$   
378 (respectively; biome-level random effects),  $\beta_{0k,j}$  and  $\beta_{1k,j}$  are taxa-level departures  
379 (nested within biomes) from  $\beta_0$  and  $\beta_1$  (taxa-level random effects),  $\beta_{0k,j,i}$  and  $\beta_{1k,j,i}$  are

380 the (nested) cell-level departures from  $\beta_0$  and  $\beta_1$  (cell-level random effects);  $y_{k,j,i,t}$  is  
381 the (rarefied) species richness in year  $t$  of the  $i$ th cell for the  $j$ th taxonomic group  
382 within the  $k$ th biome.

383

384 The species richness RCT model had the form:

385

$$\log(\mu_{j,i,t}) = \beta_0 + \beta_{0j} + \beta_{0j,i} + (\beta_1 + \beta_{1j} + \beta_{1j,i})x_{j,i,t},$$

386

$$y_{j,i,t} \sim \text{poisson}(\mu_{j,i,t}),$$

387

388 where  $x_{j,i,t}$  is the time in years,  $\beta_0$  and  $\beta_1$  are the global intercept and slope (fixed  
389 effects),  $\beta_{0j}$  and  $\beta_{1j}$  are the departures for each realm-climate-taxa group from  $\beta_0$  and  
390  $\beta_1$  (respectively; random effects),  $\beta_{0j,i}$  and  $\beta_{1j,i}$  are the cell-level departures from  $\beta_0$  and  
391  $\beta_1$  (cell-level random effects);  $y_{j,i,t}$  is the (rarefied) species richness in year  $t$  of the  $i$ th  
392 cell, of the  $j$ th combination of realm-climate-taxa.

393

394 All dissimilarity metrics were modelled assuming Gaussian error and an identity link  
395 function, resulting in BT models of the form:

396

$$\mu_{k,j,i,t} = \beta_0 + \beta_{0k} + \beta_{0k,j} + \beta_{0k,j,i} + (\beta_1 + \beta_{1k} + \beta_{1k,j} + \beta_{1k,j,i})x_{k,j,i,t},$$

397

$$y_{k,j,i,t} \sim N(\mu_{k,j,i,t}, \sigma^2),$$

398

399 where  $x_{k,j,i,t}$  is the time in years,  $\beta_0$  and  $\beta_1$  are the global intercept and slope,  $\beta_{0k}$  and  $\beta_{1k}$   
400 are the biome-level departures from  $\beta_0$  and  $\beta_1$  (respectively),  $\beta_{0k,j}$  and  $\beta_{1k,j}$  are the taxa-

401 level departures from  $\beta_0$  and  $\beta_1$ ,  $\beta_{0k,j,I}$  and  $\beta_{1k,j,I}$  are the cell-level departures from  $\beta_0$   
402 and  $\beta_1$ , and  $y_{k,j,i,t}$  is the value of the dissimilarity metric (total Jaccard dissimilarity, or  
403 one of the components) in year  $t$  of the  $i$ th cell, of the  $j$ th taxonomic group within the  
404  $k$ th biome. The dissimilarity metric was set to equal zero (perfectly similarity) for the  
405 first year of each time series.

406

407 The dissimilarity RCT models had the form:

408

$$\mu_{j,i,t} = \beta_0 + \beta_{0j} + \beta_{0j,i} + (\beta_1 + \beta_{1j} + \beta_{1j,i})x_{j,i,t},$$

409

$$y_{j,i,t} \sim N(\mu_{j,i,t}, \sigma^2),$$

410

411 where  $x_{j,i,t}$  is the time in years,  $\beta_0$  and  $\beta_1$  are the global intercept and slope,  $\beta_{0j}$  and  $\beta_{1j}$   
412 are the departures for each realm-climate-taxa group from  $\beta_0$  and  $\beta_1$  (respectively),  
413  $\beta_{0j,i}$  and  $\beta_{1j,i}$  are the cell-level departures from  $\beta_0$  and  $\beta_1$ , and  $y_{j,i,t}$  is the value of the  
414 dissimilarity metric in year  $t$  of the  $i$ th cell, of the  $j$ th combination of realm-climate-  
415 taxa. The dissimilarity metric was set to equal zero (perfectly similarity) for the first  
416 year of each time series.

417

418 We used weakly regularising normally-distributed priors for the global intercept and  
419 slope:

420

$$\beta_0 \sim N(0,5),$$

$$\beta_1 \sim N(0,2),$$

421

422 Group-level parameters were all assumed to be  $N(0, \sigma)$ , and priors on the  $\sigma$  were the  
423 same for all models of composition (the turnover and nestedness components of  
424 Jaccard's dissimilarity) and the RCT of species richness (i.e., as follows, with the  $k$   
425 subscript dropped for the RCT models):

426

$$\sigma_{\beta_{0k}} = \sigma_{\beta_{0k,j}} = \sigma_{\beta_{0k,j,i}} \sim \text{half Cauchy}(0, 2.5),$$

$$\sigma_{\beta_{1k}} = \sigma_{\beta_{1k,j}} = \sigma_{\beta_{1k,j,i}} \sim \text{half Cauchy}(0, 2.5).$$

427

428 The group-level parameters of the BT species richness model were also assumed to be  
429  $N(0, \sigma)$ , but the priors were drawn from the student  $t$  distribution:

$$\sigma_{\beta_{0k}} = \sigma_{\beta_{0k,j}} = \sigma_{\beta_{0k,j,i}} \sim \text{student } t(1, 0, 10),$$

$$\sigma_{\beta_{1k}} = \sigma_{\beta_{1k,j}} = \sigma_{\beta_{1k,j,i}} \sim \text{student } t(1, 0, 10).$$

430

431

432 Correlations between levels of the grouping-factors (e.g., taxa with biomes) are  
433 estimated using the Cholesky decomposition (L) of the correlation matrix, with a  
434 Lewandowski-Dorota-Joe (LKJ) prior<sup>50</sup>, here set as:

435

$$L \sim \text{LKJ}(2).$$

436

437 Model convergence and goodness of fit were assessed using a combination of  
438 statistics (Gelman–Rubin diagnostic<sup>51,52</sup>) and visual inspection of the Markov chains.

439

440 All data manipulation and analysis were conducted in R (3.3.1 or greater<sup>53</sup>). Models  
441 were coded using the ‘brms’ package (version 1.5.1 or greater<sup>50</sup>), which fits models  
442 with the probabilistic programming language Stan<sup>50</sup>.

#### 443 **Sensitivity analyses**

444 A recurrent criticism of existing time series analyses is the lack of an appropriate  
445 baseline from which to detect change<sup>11,54</sup>. Obtaining baselines for all of the datasets in  
446 the BioTIME database is unrealistic, but we assessed whether the rates of change are  
447 themselves changing through time by quantifying biodiversity change for different  
448 time periods (since the 1950’s). To do this, we subset the data into three periods:  
449 1951- 1970, 1971-1990, and 1990-2010, and refit each of the models to each of these  
450 subsets (Extended Data Figs. 4-6).

451

452 We also assessed the sensitivity of our estimates of biodiversity change to the length  
453 of the time series (number of discrete years sampled), and the starting year of each  
454 time series (Extended Data Fig. 10). Additionally, we examined the estimates of  
455 change as a function of the initial assemblage species richness (i.e., the number of  
456 species in the first year of each assemblage time series; Extended Data Fig. 10).

457

#### 458 **Code availability**

459 Code is available on an online archive at Zenodo: (doi:  
460 <https://doi.org/10.5281/zenodo.1475218>)

461

462

#### 463 **Data availability**

464 The time series analysed were from 332 unique references found in the BioTIME  
465 dataset and in other studies which were used with permission.

466

467 Approximately 92% (306 references) of the biodiversity studies analysed here are  
468 available as part of the published BioTIME Database<sup>28</sup>. The data are openly available,  
469 and can be accessed on Zenodo (<https://doi.org/10.5281/zenodo.1211105>) or through  
470 the BioTIME website (<http://biotime.st-andrews.ac.uk/>).

471

472 Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., and BioTIME  
473 consortium (200+ authors). 2018. BioTIME: a database of biodiversity time-series  
474 for the Anthropocene. *Global Ecology and Biogeography*. [10.1111/geb.12729](https://doi.org/10.1111/geb.12729)

475

476 The remaining 8% (26 references) of biodiversity studies analysed were used with  
477 permission. Some of these studies are published and publicly available outside of the  
478 BioTIME database, and others are available with permission from the corresponding  
479 author on reasonable request. For more details regarding the original citations,  
480 corresponding authors, and availability of these datasets, please refer to Table S1 in  
481 Dornelas et al. (2018).

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634

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655 MD conceived the project. SB, SRS, and MD led the development of the project,  
656 assisted with data analysis and interpretation, and wrote the first draft of the  
657 manuscript. SB and SRS collaborated on the core data preparation and coding the  
658 analysis in R. SB designed the analytical models and prepared the figures for the  
659 manuscript. FM managed the BioTIME database, queried it for the analysis, and  
660 provided help with figures. All authors contributed to the sDiv working group that  
661 conceived this project, to key discussions that led to the design of the study, and

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665

#### 666 **Competing Interests**

667 The authors declare no competing interests.

668

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#### 673 **Supplementary Information**

674 Further information detailing the results, including the sensitivity analysis, is available  
675 in the [Supplementary Information](#) and [Extended Data](#) files, linked to this paper.

676