

# 1 **Temperature-related biodiversity change across temperate marine and** 2 **terrestrial systems**

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23 **Abstract**

24 Climate change is reshaping global biodiversity as species respond to changing temperatures.  
25 However, the net effects of climate-driven species redistribution on local assemblage  
26 diversity remain unknown. Here, we relate trends in species richness and abundance from  
27 21,500 terrestrial and marine assemblage time series across temperate regions (23.5-60.0°) to  
28 changes in air or sea surface temperature. We find a strong coupling between biodiversity and  
29 temperature changes in the marine realm, which is conditional on the baseline climate. We  
30 detect increases in species richness with increasing temperature that is twice as pronounced in  
31 warmer locations, while abundance declines with warming in the warmest marine locations.  
32 In contrast, we did not detect systematic temperature-related richness or abundance trends on  
33 land, despite a greater magnitude of warming. We also found no evidence for an interaction  
34 between biodiversity change and latitude, further emphasizing the importance of baseline  
35 climate in structuring assemblages. As the world is committed to further warming, significant  
36 challenges remain in maintaining local biodiversity amongst the non-uniform inflow and  
37 outflow of “climate migrants” across distinct regions, especially in the ocean.

38

39 **Keywords:** temperature change, species richness, abundance, species gains, species losses,  
40 biodiversity change, climate change

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42 Climate change is driving a reorganization of ecological communities as species track  
43 changes in air and ocean temperatures. However, global warming is not unfolding evenly  
44 across the planet, and this heterogeneity is layered over the uneven distribution of  
45 biodiversity. Species benefiting from warming exhibit abundance increases and expand their  
46 geographic ranges<sup>1-5</sup>. Conversely, species that are more thermally restricted may decline with

47 warming, as individuals die or move to more suitable locations<sup>4,6,7</sup>. The latter is typically  
48 expected for tropical species, since they have narrower thermal tolerances than temperate  
49 species, and live closer to their upper thermal limits<sup>6,8-11</sup>. In contrast, mid- to high-latitudes  
50 undergoing warming may provide suitable habitat for species expanding their ranges  
51 poleward<sup>4,12</sup>. As the tropics hold the majority of the world's species<sup>13</sup>, lower-latitude  
52 temperate regions undergoing warming may experience larger increases in species richness  
53 and abundance compared to temperate locations at higher latitudes (Fig. 1). Biodiversity  
54 change may further unfold differently depending on the baseline climate, i.e. the effects of  
55 warming might differ between initially warmer *versus* colder regions<sup>3,6,12,14</sup>. For instance,  
56 warm temperate regions may offer the first habitats suitable for climate immigrants.

57 Warming-induced biodiversity change may also be relatively strong in the ocean<sup>3,15,16</sup>.  
58 Marine species are highly responsive to temperature change and can track changing isotherms  
59 with fewer barriers to dispersal, compared to terrestrial species<sup>3,14-19</sup>. Moreover, the  
60 availability of thermal microrefugia is limited in the ocean, while in terrestrial ecosystems  
61 organisms can seek shade or burrow in soil to buffer the effects of warming<sup>17,20</sup>. Therefore,  
62 the effects of temperature change are expected to be more immediate and directly detected for  
63 marine ecosystems, an expectation which is supported by a growing literature which has  
64 quantitatively compared the responses of individual species between marine and terrestrial  
65 realms<sup>3,14-16</sup>. However, the net effects of temperature-related species' movements and  
66 abundance changes on assemblage-level diversity have not yet been systematically quantified  
67 across realms.

68 Here, we quantify temperature-related species richness and total abundance change in marine  
69 and terrestrial assemblages across temperate regions of the planet (23.5°-60.0° absolute  
70 latitude). Specifically, we test two predictions for the effects of temperature change on  
71 assemblage-level diversity: (1) species richness and total abundance will increase with

72 warming, and such increases will be greatest across relatively warm regions that border the  
73 species-rich tropics; and (2) the coupling of assemblage and temperature change will be  
74 tighter in the ocean than on land. We focus on assemblage-level trends rather than species-  
75 specific responses, and quantify changes in both total abundance and species richness. These  
76 two metrics can be decoupled from each other, and abundance is typically more responsive  
77 than richness<sup>21,22</sup>. We further disentangle richness change into species gains and losses to  
78 better understand the underlying dynamics of temperature-related biodiversity change. To test  
79 our expectations, we used the largest database of assemblage time series, BioTIME<sup>23</sup>, which  
80 includes studies for plants, invertebrates, birds, mammals, and fish, to quantify biodiversity  
81 trends. These assemblages consist of co-occurring species systematically sampled through  
82 time. Since spatial extent varied among studies in BioTIME, we harmonized the biodiversity  
83 observations to a common spatial resolution to minimise the influence of variation in spatial  
84 extent on our results<sup>24</sup>; this allowed us to quantify the effect of temperature change at a  
85 standardised resolution across regions and realms. We first estimated trends in biodiversity  
86 and temperature separately, and then quantified the relationships between the two.

87 Specifically, for each study we allocated individual samples to 96 km<sup>2</sup> hexagonal grid cells  
88 based on their location (Methods; <sup>24</sup>). For studies with large extents, we created new equal-  
89 extent assemblage time series by allocating the samples to different grid-cell by study  
90 combinations (thus keeping the integrity of each sample and study within each grid cell). We  
91 used these new spatially harmonized assemblage time series in our analysis, selecting data  
92 from temperate regions only (since these are the better sampled regions within BioTIME).  
93 We then selected time series with at least five years of sampling (mean=9.2 years), yielding  
94 21,500 assemblage time series across both realms (19,875 marine and 1,625 terrestrial from  
95 156 original studies; Fig. S1, Table S1). Because the number of samples can vary from year  
96 to year within each time series, we used sample-based rarefaction to equalise sampling effort

97 among years and then quantified trends in richness, total abundance, and number of species  
98 gains and losses. For the same locations and for the time spans matching the duration of the  
99 biodiversity monitoring periods, we extracted mean monthly temperature records from  
100 HadCRUT4<sup>25,26</sup> and estimated the corresponding rates of sea surface or air temperature  
101 change per year. We then quantified the relationships between changes in biodiversity and  
102 changes in temperature with meta-analytical Bayesian hierarchical models, allowing  
103 responses to vary among taxonomic groups. To test our expectations, we included an  
104 interaction term between temperature change and latitude or long-term average temperature  
105 (i.e. baseline climate) in our models, fitted separately for the marine and terrestrial realms.

106

## 107 **Results**

108 Temperature trends were highly variable, with locations at similar latitudes exhibiting  
109 different directions and magnitudes of change (Fig. 2a). Yet, both sea surface and air  
110 temperatures increased on average at the locations and time periods of our study, even though  
111 the majority of our time series spanned less than 10 years. The warming signal was more  
112 pronounced on land than in the ocean (Fig. 2b; average mean temperature change rate was  
113 0.022 °C/year on land, *versus* 0.012 °C/year in the ocean).

114 Biodiversity change was also highly variable among the assemblage time series (Fig. 2c).  
115 Yet, despite the variability in both temperature and biodiversity trends, coherent  
116 macroecological signals emerged, but only in the ocean and conditional on the baseline  
117 climate (Fig. 3, Table S2). In the marine realm, we found an overall increase in species  
118 richness with warming that was twice as pronounced in warmer locations, underpinned by  
119 higher rates of species gains and lack of systematic changes in species losses (Figs. 3, 4 and  
120 S2). Additionally, warming coincided with losses of individuals in the warmest marine

121 locations, whereas cooler locations tended to gain individuals with increasing temperature  
122 (Figs. 3, 4 and S2). In contrast, no systematic biodiversity responses emerged on land, where  
123 the 95% credible intervals overlapped zero for all the biodiversity metrics included (Fig. 3,  
124 Table S2). Our analysis clearly highlights the fundamental role of climate baselines in  
125 modulating biodiversity responses (particularly in the ocean), given that latitude showed no  
126 or very weak interacting effects with temperature change (Fig. S3).

127 The different responses between the two realms were robust to uneven sampling in terms of  
128 number of locations and latitudinal range (Fig. S4). Our results were also consistent across  
129 different temperature variables (long-term annual and maximum temperature, and annual  
130 mean temperature of the first year) and between different temperature databases for  
131 quantifying climate baselines (Fig. S3; see Methods).

132

### 133 **Discussion**

134 We reveal striking differences in warming-related biodiversity change between marine and  
135 terrestrial realms, with a much stronger signature of warming on marine assemblages. Our  
136 results are unlikely due to confounding factors, given that climate change is poorly spatially  
137 correlated with other anthropogenic drivers of change for both marine and terrestrial realms<sup>27</sup>.  
138 Further, temperature is expected to be a strong driver of biodiversity change<sup>28-30</sup>.

139 The warming-related increase in marine species richness is consistent with the expectation  
140 that as the Earth's climate warms, temperate regions undergoing warming will receive an  
141 influx of species tracking suitable temperatures, and increases in warm-affinity  
142 generalists<sup>2,7,8,18,28</sup>. This warming-related increase in species richness is likely, in part,  
143 underpinned by species from lower latitudes shifting their ranges poleward to avoid  
144 exceeding their upper thermal limits<sup>4,12</sup>. Indeed, projected rates of extirpation in response to

145 recent and future warming are highest for tropical marine species<sup>8,31</sup>. Here, we found that  
146 species gains outpaced losses in the warmest locations in the ocean where temperature has  
147 also increased. This finding is consistent with asymmetrical responses between species range  
148 edges, with faster colonisations expected following climatic niche expansion, and with slower  
149 local extinctions linked to delayed responses at species trailing edges<sup>3,4</sup>. The prevailing influx  
150 of species with warming is likely to lead to novel biotic communities and interactions as  
151 species distributions are re-shuffled, with potentially far-reaching consequences for  
152 ecosystems functioning<sup>3,8,31,32</sup>.

153 Our results further highlight that substantial loss of individuals can occur simultaneously with  
154 increases in richness, illustrating that temperature-related changes in richness and abundance  
155 can be decoupled. Abundance declines may be occurring for more thermally restricted  
156 species, owing to reduced performance and population declines, as critical thermal thresholds  
157 are crossed<sup>4,6,7</sup>, for instance related to the adverse effects of increasing temperatures on  
158 metabolic rates and primary production<sup>28,33</sup>. Influxes of climate immigrants can also drive  
159 local declines in populations due to greater grazing and predation rates, e.g.<sup>34,35</sup>. The  
160 abundance declines across our warmest locations in the ocean suggest warming-related  
161 destabilization of populations possibly reflecting reductions in the carrying capacity of  
162 marine ecosystems.

163 We also find strong modulating effects of baseline climatic conditions on both abundance and  
164 richness responses that are not attributable to latitude *per se*. These findings highlight that  
165 rising temperatures in locations that are already warm in comparison to other regions from  
166 similar latitudes can lead to greater assemblage restructuring. This may reflect the patchiness  
167 in temperature regimes across similar latitudes, for example due to altitudinal or depth  
168 gradients, proximity to the coast, or ocean currents. The baseline climate therefore emerges as  
169 a major predictor of temperature-related biodiversity change in marine systems.

170 Overall, and despite faster warming on land, terrestrial assemblages did not show systematic  
171 responses in richness or abundance with temperature change. The stronger responses  
172 observed for marine assemblages are consistent with reported faster range shifts in the ocean  
173 and higher sensitivity of marine organisms to temperature change compared to terrestrial  
174 species<sup>3,12,14–16</sup>. Our findings are also consistent with warming-related local extirpations being  
175 twice as common in the ocean as on land<sup>15</sup>. The lack of systematic assemblage-level change  
176 associated with warming on land might be due to greater thermoregulation capacity and  
177 wider thermal safety margins of terrestrial taxa<sup>9,15,16</sup>. Additionally, compared to seascapes,  
178 higher landscape complexity enables terrestrial species to exploit thermal microhabitats, thus  
179 allowing for the persistence of local populations for longer periods<sup>9,20</sup>. Indeed, access to  
180 thermal refugia was reported to be a fundamental factor underlying the relatively low  
181 vulnerability of terrestrial ectotherm species to warming, and emphasizes the potential  
182 deleterious combined effects of warming and land-use changes<sup>15</sup>. Finally, a weaker link  
183 between assemblage responses and temperature change on land may be due to other factors,  
184 such as land-use change and moisture availability, posing stronger constraints on local  
185 biodiversity. Nonetheless, the smaller magnitude or slower responses of terrestrial species to  
186 temperature change<sup>5,12,15,24,36,37</sup>, combined with the faster rates of warming on land, indicate a  
187 potentially higher risk of climatic debt (i.e. response lags) among terrestrial *versus* marine  
188 taxa<sup>3,12,14,19,36,38–40</sup>. Additional research with higher-resolution temperature data matching the  
189 scale of organisms' responses is needed to better quantify terrestrial assemblages responses to  
190 temperature change, and these developments remain a major challenge for many different  
191 taxa.

192 Our analyses provide a first step towards explaining divergent patterns of assemblage-level  
193 biodiversity change across the planet<sup>24,41</sup>. Overall, our results provide strong support the  
194 prediction that divergent biodiversity trajectories across latitude may arise as a consequence



195 of global warming, with polar and temperate regions likely acting as “sinks”, and tropical  
196 regions as “sources”<sup>6,8,31</sup>. In turn, these responses could prompt a shift in the latitudinal  
197 diversity gradient towards higher latitudes, with faster rates of change in the ocean. While we  
198 focused here on temperate regions, tropical and polar biomes are predicted to undergo severe  
199 restructuring in response to temperature change, albeit along different trajectories<sup>6,8,12</sup>.  
200 However, lack of sufficient biodiversity monitoring data for tropical and polar systems<sup>23,42</sup>  
201 hampers a comprehensive assessment of assemblage-level responses to temperature change in  
202 these regions.

203 Future global warming impacts on biodiversity are likely to exceed and potentially diverge  
204 from the changes revealed here<sup>8,31,33,43–45</sup>. Indeed, initial increases in richness and abundance  
205 in response to warming may be followed by losses if warming continues<sup>7,46,47</sup>. These declines  
206 in marine systems may affect food security and livelihoods of human populations that depend  
207 on the ocean<sup>7,48</sup>. Additionally, while a consistent signal of temperature change was not  
208 evident on land, future impacts on terrestrial assemblages are expected from continuing rising  
209 temperatures, extreme heat events, fires, and lack of moisture<sup>33,44,49</sup>. Because the Earth is  
210 committed to further warming, a systematic reduction of greenhouse gas emissions alongside  
211 efforts to further prevent habitat loss and improve habitat connectivity will be fundamental to  
212 allow species to track suitable climates across increasingly impacted land- and seascapes and  
213 to avoid severe biodiversity disruption and loss.

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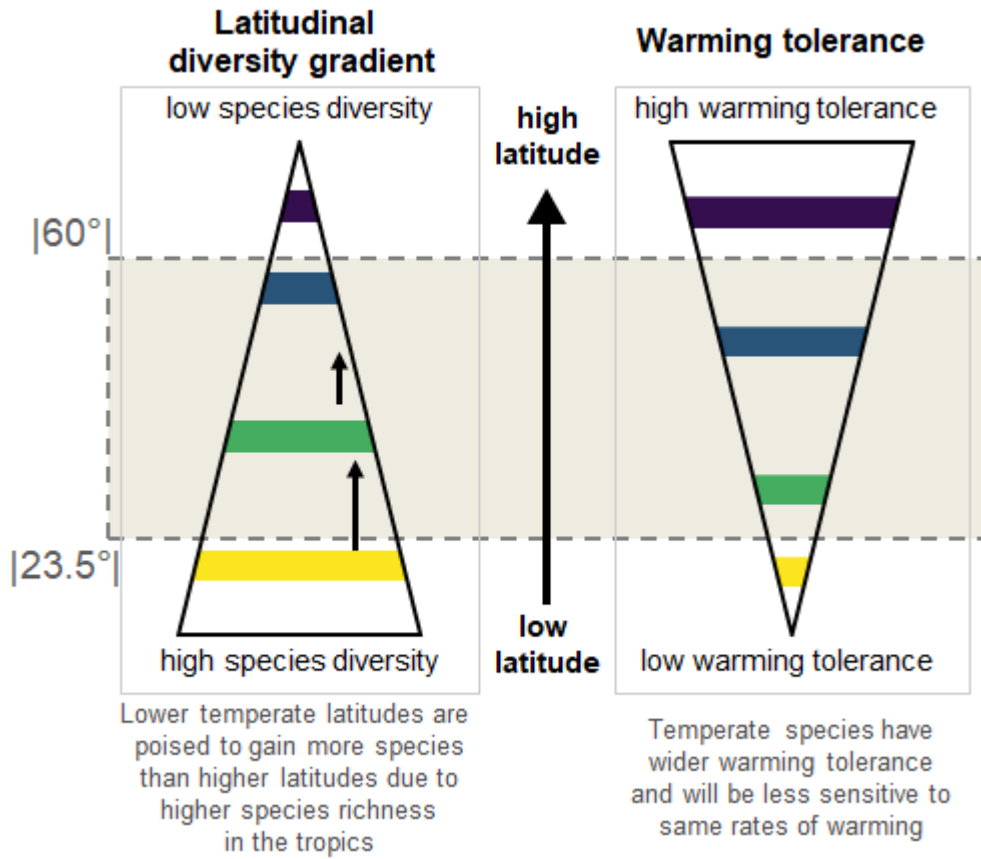
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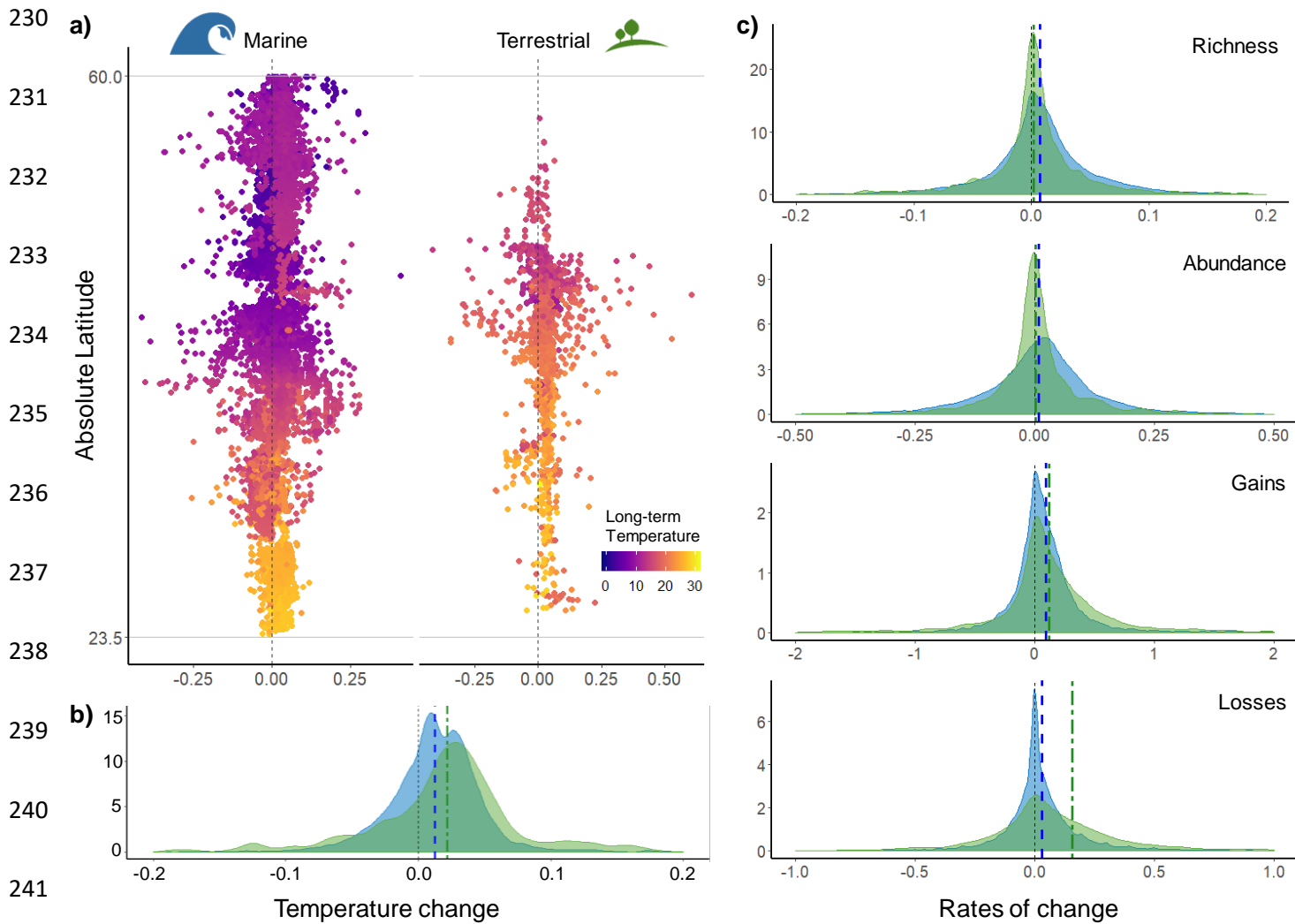
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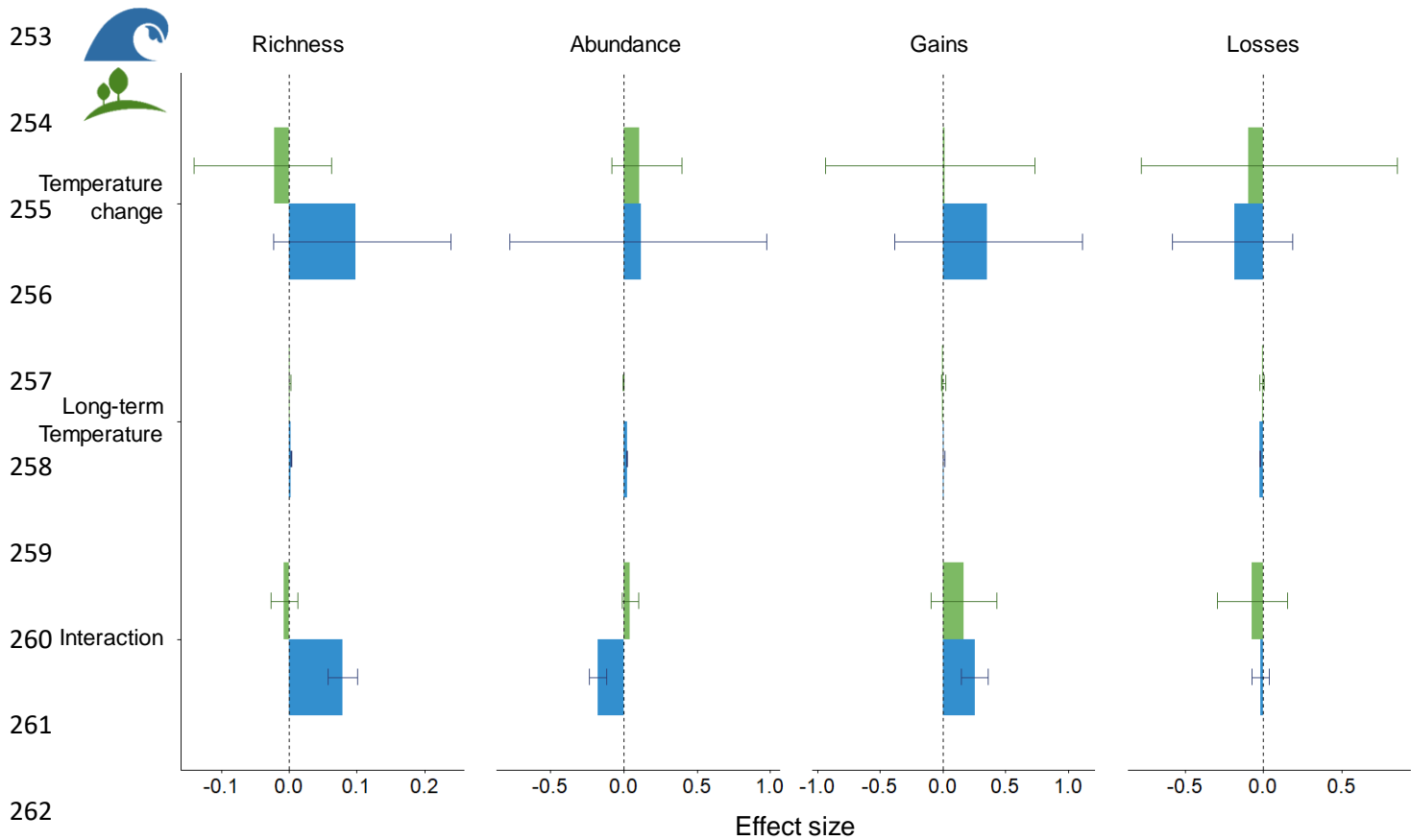
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**Figure 1. Mechanisms underpinning the expectation that temperature-related biodiversity change unfolds unevenly across the planet** (within the temperate latitudinal band where our data fall), stemming from the latitudinal gradients in species diversity (decrease with latitude) and species warming tolerances (or thermal safety margins (TSM); increase with latitude).

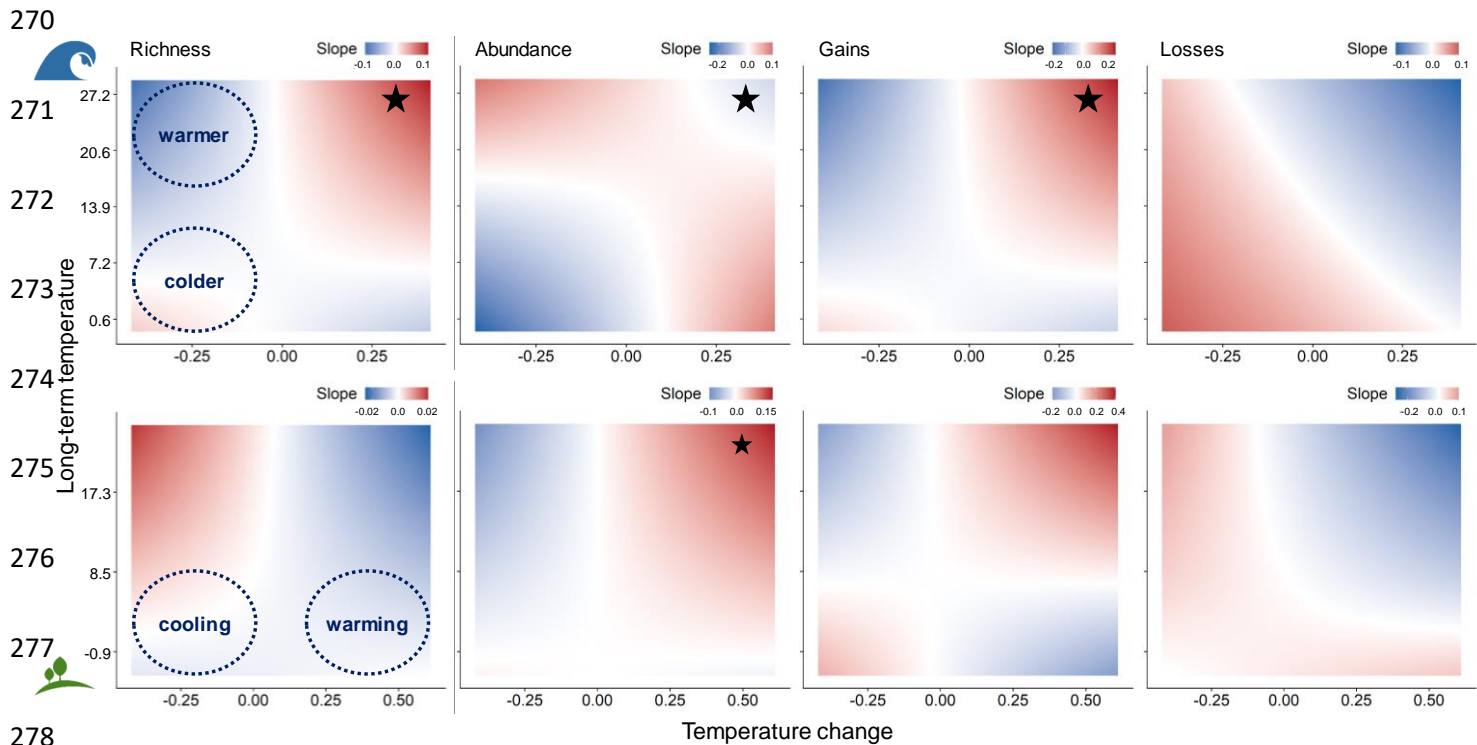


242 **Figure 2. Variation in temperature and local biodiversity trends across the time series**

243 (marine in blue,  $n=19,875$ ; terrestrial in green,  $n=1,625$ ). (a) Each point indicates the rate of  
244 temperature change ( $^{\circ}\text{C}/\text{year}$ ) for a specific time series, coloured according to the long-term  
245 average temperature. There was no clear latitudinal pattern in temperature change: while the  
246 majority of locations in both realms experienced warming, and more so for terrestrial  
247 locations (b), many locations experienced cooling during the period examined. Local  
248 biodiversity change estimates (rate/year) also exhibited wide variability (c) (note the different  
249 scales for the different metrics; x-axes were truncated to improve clarity). Tick dashed  
250 vertical lines indicate the overall mean per realm in all the density plots. The biodiversity  
251 time series locations cover numerous habitats and biomes (Fig. S1), and sample a large range  
252 of the planet's long-term average temperature gradient.



263 **Figure 3. Biodiversity responses to the interacting effects of temperature change and**  
264 **long-term average temperature (i.e. baseline climate).** Marine locations (blue) exhibited  
265 stronger responses compared to terrestrial locations (green), while baseline climate  
266 modulated these responses in divergent directions. Bars represent the effect sizes and  
267 whiskers indicate the 95% credible intervals estimated from the Bayesian meta-analysis (note  
268 the different scales for the different metrics); estimated parameters were considered to  
269 represent signals in the responses when the credible intervals did not include zero (Table S2).



279 **Figure 4. Biodiversity responses to temperature change across different baseline**

280 **climates.** Each panel depicts the rate and direction of biodiversity change depending on the  
281 temperature change experienced (cooling *versus* warming) and on the long-term average  
282 temperature (colder *versus* warmer), where red indicates positive slopes for the biodiversity  
283 response, and blue indicates negative slopes (note the different scales across the different  
284 metrics), for marine (top row) and terrestrial realms (bottom row). Stars indicate when the  
285 95% credible intervals for the interaction term from the meta-analytical models did not  
286 overlap zero (Fig. 3, Table S2; smaller star for abundance change on land indicates 95% CI  
287 marginally overlapping zero).

## 288 **Methods**

### 289 Biodiversity data and trends

290 BioTIME<sup>23</sup> is currently the largest global database of assemblage time series, including 386  
291 individual studies (Study ID; plus extended data sources) across different taxonomic groups,  
292 holding over 12 million records of abundance for over 45 thousand species. For this analysis,  
293 we only included studies reporting counts of individuals per species in terrestrial and marine  
294 systems. We excluded freshwater studies as these are too few to confidently analyse  
295 biodiversity trends across taxa and different regions.

296 Each study is comprised of distinct samples (i.e. individual plots, transects, tows, etc.  
297 sampled at a given time), and the number of samples can vary among years within each  
298 study. As the spatial extent varies among studies, we gridded those studies that had large  
299 extents and multiple sampling locations into hexagonal cells of  $\sim 96\text{km}^2$ ; many studies were  
300 not partitioned because they were contained within a single cell<sup>24</sup>. Specifically, each sample  
301 was assigned to different combinations of study ID x grid cell based on their latitude and  
302 longitude, resulting in new assemblage time series (each with multiple samples across years).  
303 These new time series were given a unique identifier that was the concatenation of the study  
304 ID and the grid cell reference number, and thus contained samples from only one study – i.e.  
305 the integrity of each study and each sample were maintained. This process allowed us to  
306 relate biodiversity and temperature trends at a standardized resolution. To minimise the effect  
307 of unobserved species on estimates of biodiversity change, we calculated the abundance-  
308 based coverage<sup>50</sup> of each annual sample within each time series, and removed all samples  
309 with coverage less than 0.85. To be able to estimate reliable biodiversity trends, we restricted  
310 our analysis to time series sampled in at least five years (not necessarily consecutive).  
311 Because the number of samples can vary among years, we used sample-based rarefaction<sup>51</sup> to  
312 standardise the number of samples among years for each time series before calculating the

313 biodiversity metrics. Specifically, we identified the minimum number of samples taken in  
314 each year within each assemblage time series; this minimum was then used to randomly  
315 sample each year down to that number of samples. Finally, given the paucity of data  
316 representing polar and tropical regions, we excluded these regions (based on absolute  
317 latitudinal cut-offs at 60° and 23.5°, respectively). This process yielded 21,500 assemblage  
318 time series representing 156 original studies (Table S1) between 1900 and 2016, across  
319 19,875 marine and 1,625 terrestrial locations. The average number of years sampled across  
320 the time series was 9.2 years, with the longest time series spanning 97 years (Fig. S5).

321 To quantify rates of biodiversity change, we calculated linear trends over time for species  
322 richness (logS), total abundance (logN), number of species gains and species losses. Counts  
323 of gains and losses retained species identity information, and were quantified based on  
324 comparison with the first year sampled in each time series. For losses, a positive slope means  
325 the number of species lost from a location is increasing through time; negative slopes  
326 represent time series where the magnitude in species losses decreased over time. We repeated  
327 the sample-based rarefaction process described above 199 times for each time series,  
328 recorded the values and took the median for each biodiversity metric in each year, in order to  
329 reduce the effect of any outlier samples on our estimates. We used ordinary least squares  
330 regression because we were interested in the long-term direction and magnitude of the  
331 biodiversity trends, and to allow us to compare the rates of change among locations, realms  
332 and metrics. We retained the estimated slope and standard error for each time series for use in  
333 our second-stage meta-analytic models.

334

335

336 Temperature data and trends

337 We focus on temperature as a climate variable because of its influence on every level of  
338 biological organization, from individual metabolic rates to ecological communities' dynamics  
339 and structure<sup>28-30</sup>. We extracted temperature records from HadCRUT4<sup>25,26</sup>, specifically the  
340 HadSST3 data for marine Sea Surface Temperature (SST) on a 1° resolution, and the  
341 CRUTEM4 data for air temperature on land on a 0.5° resolution. We did not harmonize the  
342 spatial resolution between the two data sources because we wanted to use the best available  
343 data in each realm. For the location of each biodiversity time series, we extracted monthly  
344 mean temperature records for the duration of the biodiversity monitoring period  
345 ( $Year_{start}:Year_{end}$ ), and estimated mean temperature trends using generalized additive models  
346 (GAM), including a temporally autocorrelated error structure (package *mgcv*<sup>52</sup>). This also  
347 allowed us to assess if accounting for seasonality within years would improve model  
348 performance. We used AIC to compare models with and without “month”, selecting the best  
349 model for each time series. We extracted the linear slope from the model, which summarises  
350 the trend for mean annual temperature change.

351 To test if biodiversity responses to temperature change were modulated by the baseline  
352 climate at any given location, we extracted annual mean temperature data from the  
353 WorldClim<sup>53</sup> database for terrestrial time series, and from the Bio-ORACLE database<sup>54,55</sup> for  
354 marine time series (on a resolution of 0.01° for terrestrial and of 0.1° for marine systems,  
355 respectively). For each realm, we standardized the long-term annual mean temperature across  
356 all the locations by subtracting the mean and dividing by the standard deviation.

357

358



359 Meta-analysis

360 Having estimated the trends for biodiversity and temperature independently for each individual  
361 time series, we assessed the effect of temperature change on the rates of change of each  
362 biodiversity metric in a second-stage analysis. We employed a meta-analytical Bayesian  
363 framework using the package brms<sup>56,57</sup> (version 2.6.0), and fitted generalized linear models to  
364 each realm separately, having initially evaluated that there was an effect of realm when fitting  
365 a full model. All models were created using the Stan computational framework ([http://mc-](http://mc-stan.org/)  
366 [stan.org/](http://mc-stan.org/)) accessed via brms. To determine whether the baseline climate modulated the  
367 biodiversity responses, models were fit with an interaction term between temperature change  
368 and the long-term average temperature at each location. Additionally, we fitted similar models  
369 using latitude. We used two random effect terms: one allowing for different slopes per  
370 taxonomic group (Taxon), and another allowing for different intercepts per study ID nested  
371 within Taxon. This allowed us to account for: 1) potentially different responses to temperature  
372 change among taxa; 2) differences in species richness among taxa, as well as different  
373 assemblage time series originating from the same study, and different studies monitoring the  
374 same taxonomic groups across the BioTIME database, respectively; and 3) spatial  
375 autocorrelation. The different taxonomic groups were informed by the original data sources  
376 metadata, and were: "Amphibians", "Benthos", "Birds", "Fish", "Mammals", "Marine  
377 invertebrates", "Terrestrial invertebrates", "Terrestrial plants", and "All - several major  
378 groups".

379 The overall model structure implemented for each realm was:

380  $\Delta \text{Biodiversity} \sim 0 + \Delta \text{Temperature} * \text{Long-term average temperature} +$

381  $(0 + \Delta \text{Temperature} \mid \text{Taxon}) + (1 \mid \text{Taxon}/\text{StudyID}).$

382 Additionally, brms allows to specify known standard errors for performing meta-analysis  
383 using the function `se()` when specifying the formula for the models<sup>56,57</sup>, using the syntax:  
384  $\Delta\text{Biodiversity} \mid \text{se}(\Delta\text{Biodiversity}, \text{sigma} = \text{TRUE})$ .

385

386 Models were run using 4 chains, each with 8000 iterations, with a warm up of 4000 and non-  
387 informative flat priors. Stan implements Hamiltonian Monte Carlo and its extension, the No-  
388 U-Turn Sampler (NUTS) algorithms, which converge quickly<sup>56</sup>. Convergence was assessed  
389 by visually examining trace plots and using Rhat values (the ratio of the effective sample size  
390 to the overall number of iterations, with values close to one indicating convergence)<sup>56</sup>. All the  
391 analyses were run in R version 4.3.1<sup>58</sup>.

392

393

394 Sensitivity analysis

395 To evaluate the robustness of potential interactions with the baseline climate, we additionally  
396 ran our models with two alternative baseline temperature variables. To that end, we extracted  
397 the variables “Mean Temperature of Warmest Quarter” from WorldClim and “Long-term  
398 maximum sea surface temperature” from Bio-ORACLE, as well as the average temperature  
399 in the first year sampled for each biodiversity time series from the same dataset that was used  
400 to quantify the trends (i.e. the spatially less resolved HadCRUT4 dataset).

401 To evaluate whether uneven sampling could be driving the observed differences between the  
402 marine and terrestrial realms, we fitted models to subsets of the marine data that matched  
403 both the number of locations (1,625 time series) and the latitudinal range of the terrestrial  
404 data. We did not attempt to control for temperature change differences between realms  
405 because this is part of the signal to be modelled. We fitted the meta-analytical models to 100

406 random subsamples for each biodiversity metric, illustrating that the estimates for the marine  
407 realm are robust (Fig. S4). We further evaluated that biodiversity responses did not show any  
408 clear pattern as a function of the number of years sampled, illustrating that the duration of  
409 sampling is unlikely to drive our findings (Fig. S6).

410 We initially explored biodiversity change patterns in response to temperature change using all  
411 the assemblage time series with at least five years of sampling – i.e. including tropical and  
412 polar locations, yielding 22,119 time series from 179 original studies (Table S1). However,  
413 the paucity of tropical and polar locations would prevent us from reliably assessing  
414 biodiversity trends in those regions; therefore, we decided to exclude these regions from the  
415 analysis and focus on the subtropical and temperate regions, where we have most data.

416

## 417 **References**

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## 558 **Contributions**

559 M.D. and A.M.S. conceived the idea, and all authors contributed to design the project. L.H.A.  
560 analysed the data in close consultation with S.A.B., A.E.B., M.D. and A.M.S.. L.H.A. wrote  
561 the first draft of the manuscript, with substantial input from A.E.B., M.D. and A.M.S.; all  
562 authors contributed to manuscript completion and revision. M.D. and A.M.S. are shared  
563 senior authors.

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## 566 **Competing interests**

567 The authors declare no conflict of interest.

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575 **Data Deposition Statement**

576 All the data can be accessed through the BioTIME database on Zenodo

577 (<https://doi.org/10.5281/zenodo.1211105>) or through the BioTIME website ([http://biotime.st-](http://biotime.st-andrews.ac.uk/)

578 [andrews.ac.uk/](http://biotime.st-andrews.ac.uk/)). Code will be made available upon publication.

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