

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

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23

24 **Abstract**

25 Climate change is reshaping global biodiversity as species respond to changing temperatures.  
26 However, the net effects of climate-driven species redistribution on local assemblage  
27 diversity remain unknown. Here, we relate trends in species richness and abundance from  
28 21,500 terrestrial and marine assemblage time series across temperate regions (23.5-60.0°  
29 latitude) to changes in air or sea surface temperature. We find a strong coupling between  
30 biodiversity and temperature changes in the marine realm, where species richness mostly  
31 increases with warming. However, biodiversity responses are conditional on the baseline  
32 climate, such that in initially warmer locations richness increase is more pronounced, while  
33 abundance declines with warming. In contrast, we do not detect systematic temperature-  
34 related richness or abundance trends on land, despite a greater magnitude of warming. As the  
35 world is committed to further warming, significant challenges remain in maintaining local  
36 biodiversity amongst the non-uniform inflow and outflow of “climate migrants”.  
37 Temperature-driven community restructuring is especially evident in the ocean, whereas  
38 climatic debt may be accumulating on land.

39

40 **Main text**

41 Climate change is driving a reorganization of ecological communities as species track  
42 changes in air and ocean temperatures<sup>1-3</sup>. However, global warming is not unfolding evenly  
43 across the planet, and this heterogeneity is layered over the uneven distribution of  
44 biodiversity. Populations of thermally restricted species may decline with warming, as  
45 individuals die, fail to reproduce or move to more suitable locations<sup>4-6</sup>. Indeed, declines are  
46 typically expected for tropical species, since they have narrower thermal tolerances than

47 temperate species, and live closer to their upper thermal limits<sup>5,7-10</sup>. In contrast, species  
48 benefiting from warming may exhibit abundance increases and expand their geographic  
49 ranges<sup>1-4,11</sup>. Thus, mid- to high-latitudes undergoing warming may provide suitable habitat  
50 for species expanding their ranges poleward<sup>4,12</sup>. As the tropics hold the majority of the  
51 world's species<sup>13</sup>, lower-latitude warming temperate regions may experience larger increases  
52 in species richness and abundance compared to temperate locations at higher latitudes, due to  
53 a larger source pool of climate immigrants (Fig. 1). Biodiversity change may further depend  
54 on the baseline climate, i.e. within latitudinal bands the effects of warming might differ  
55 between initially warmer *versus* colder regions<sup>3,5,12,14</sup>. For instance, warmer temperate regions  
56 may offer greater habitat suitability for climate immigrants from lower latitudes.

57 Warming-induced biodiversity change may also be stronger in the ocean than on land<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> (Fig. 1).  
62 Therefore, biodiversity responses to temperature change are expected to be more immediate  
63 and directly detectable for marine ecosystems; this expectation is supported by a growing  
64 literature which has quantitatively compared individual species' responses to temperature  
65 change between marine and terrestrial realms<sup>3,14-16</sup>. However, the net effects of temperature-  
66 related species' movements and abundance changes on assemblage-level diversity have not  
67 yet been systematically investigated 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; Fig. S1). Specifically, we test two predictions for the effects of temperature change  
71 on 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. These predictions are informed by the interaction between  
75 the latitudinal gradients in species richness and warming tolerance, and the differences  
76 between realms regarding environmental heterogeneity and species distribution shifts (Fig.  
77 1).

78 We focus on local assemblage-level trends, rather than species-specific responses, and  
79 quantify changes in both total abundance and species richness. These two metrics can be  
80 decoupled from each other, and abundance is typically more responsive to environmental  
81 change than richness<sup>21,22</sup>. We further disentangle richness change into species gains and  
82 losses to better understand the underlying dynamics of temperature-related biodiversity  
83 change. To test our expectations, we used the largest database of assemblage time series,  
84 BioTIME<sup>23</sup>, which includes studies of plants, invertebrates, birds, mammals, and fish. These  
85 assemblages consist of co-occurring species systematically sampled through time. Since  
86 spatial extent varies among studies in BioTIME, we harmonized the biodiversity observations  
87 to a common spatial resolution to minimise the influence of variation in spatial extent on our  
88 results<sup>24</sup>; this allowed us to quantify the effect of temperature change at a standardised  
89 resolution across regions and realms. We first estimated trends in biodiversity and  
90 temperature separately, and then quantified the relationships between the two.

91 Specifically, for each study we allocated individual samples to 96 km<sup>2</sup> hexagonal grid cells  
92 based on their location (Methods; <sup>24</sup>); i.e., each sample was assigned to a specific  
93 combination of study ID and grid cell based on its latitude and longitude, resulting in equal-  
94 extent assemblage time series with multiple samples across years. Each time series contained  
95 samples from only one study, thus the integrity of sampling methods within each study was  
96 maintained. We used these spatially harmonized assemblage time series in our analysis,

97 selecting data from temperate regions only (since these are the better sampled regions within  
98 BioTIME). We then selected time series with at least five years of sampling (mean=9.2  
99 years), yielding 21,500 assemblage time series across both realms (19,875 marine and 1,625  
100 terrestrial from 156 original studies; Figs. S1 and S2, Table S1). Because the number of  
101 samples can vary from year to year within each time series, we used sample-based  
102 rarefaction<sup>25</sup> to equalise sampling effort among years and then quantified trends in richness,  
103 total abundance, and number of species gained or lost. For the same locations and for the time  
104 spans matching the duration of the biodiversity monitoring periods, we extracted mean  
105 monthly temperature records from HadCRUT4<sup>26,27</sup> and estimated the corresponding rates of  
106 sea surface or air temperature change per year. We then quantified the relationships between  
107 changes in biodiversity and changes in temperature with meta-analytical Bayesian  
108 hierarchical models, allowing responses to vary among taxonomic groups. To test our  
109 expectations, we included an interaction term between temperature change and long-term  
110 average temperature (i.e., baseline climate) or latitude in our models, fitted separately for the  
111 marine and terrestrial realms.

112

## 113 **Results**

114 Temperature trends were highly variable, with locations at similar latitudes exhibiting  
115 different directions and magnitudes of change (Fig. 2a). Yet, both sea surface and air  
116 temperatures increased on average across the locations and time periods of our study, even  
117 though the majority of our time series spanned less than 10 years (Fig. S2). The warming  
118 signal was more pronounced on land than in the ocean (Fig. 2b; the average mean  
119 temperature change rate was 0.022 °C year<sup>-1</sup> on land, *versus* 0.012 °C year<sup>-1</sup> in the ocean).

120 Biodiversity change was also highly variable among the assemblage time series (Fig. 2c).  
121 Yet, despite the variability in both temperature and biodiversity trends, coherent  
122 macroecological signals emerged in the marine realm (Fig. 3, Table S2). We found an overall  
123 positive relationship between warming and species richness, but conditional on the baseline  
124 climate. Species richness increases were more pronounced in initially warmer locations (as  
125 indicated by the positive interaction effect), and underpinned by higher rates of species gains,  
126 while there was no detectable signal for species losses (Figs. 3, 4 and S3). Additionally,  
127 warming coincided with losses of individuals in the warmest marine locations, whereas  
128 cooler locations tended to gain individuals with increasing temperature (Figs. 3, 4 and S3). In  
129 contrast, no systematic biodiversity responses emerged on land, where the 95% credible  
130 intervals overlapped zero for all the biodiversity metrics included (Fig. 3, Table S2).

131 Our analysis highlights the fundamental role of climate baselines in modulating biodiversity  
132 responses in the ocean, given that latitude showed no or very weak interacting effects with  
133 temperature change (Fig. S4). Further tests revealed only a weak correlation between either  
134 baseline climate or latitude and temperature change (Spearman's rank correlation  $\rho = 0.063$   
135 and  $0.098$ , respectively). As such, the correlation structure of our covariates is unlikely to  
136 bias our results towards a positive effect of temperature change when combined with baseline  
137 climate rather than latitude.

138 Our results were highly robust to a number of further sensitivity tests addressing biases in the  
139 BioTIME dataset, differences amongst covariates, and model structure. We found similar  
140 responses in the marine realm when using subsets of the marine data that match the number  
141 of locations and latitudinal range of the terrestrial data, despite increased uncertainty in model  
142 estimates (Fig. S5). Our results were consistent across different baseline temperature  
143 variables (long-term annual and maximum temperature, and annual mean temperature of the  
144 first year) and between different temperature databases for quantifying climate baselines (Fig.

145 S4; see Methods). Additionally, we did not detect any systematic effect of the number of  
146 years sampled, temporal duration or start year of the time series on the estimated rates of  
147 biodiversity change (Figs. S6 and S7). Finally, there was no evidence for systematic  
148 differences in biodiversity responses among the different taxonomic groups (as estimated via  
149 the random slope model components; Figs. S8 and S9; complete model outputs with posterior  
150 estimates are shown in Tables S3-S6).

151

## 152 **Discussion**

153 We reveal striking differences in warming-related biodiversity change between marine and  
154 terrestrial realms across temperate regions, with a much stronger signature of warming on  
155 marine assemblages. Our results are unlikely due to confounding factors, given that climate  
156 change is poorly spatially correlated with other anthropogenic drivers of change for both  
157 marine and terrestrial realms<sup>28</sup>. Further, temperature is expected to be a strong driver of  
158 biodiversity change given its fundamental role in biological processes<sup>29–31</sup>.

159 The warming-related increase in local marine species richness is consistent with the  
160 expectation that as the Earth's climate warms, temperate regions undergoing warming will  
161 receive an influx of species tracking suitable temperatures, and increases in warm-affinity  
162 generalists<sup>2,6,7,18,29</sup>. This warming-related increase in species richness is likely, in part,  
163 underpinned by species from lower latitudes shifting their ranges poleward to avoid  
164 exceeding their upper thermal limits<sup>4,12,14</sup>. Indeed, projected rates of extirpation in response to  
165 recent and future warming are highest for tropical marine species<sup>7,32</sup>, which in turn are better  
166 able to track changing isotherms<sup>14</sup>. Here, we find that species gains outpaced losses in the  
167 warmest temperate locations in the ocean where temperature has also increased. This finding  
168 is consistent with asymmetrical responses between species range edges, with faster

169 colonisations expected following climatic niche expansion, and with slower extirpations  
170 linked to delayed responses at species trailing edges<sup>3,4</sup>. The prevailing influx of species with  
171 warming is likely to lead to novel biotic communities and interactions as species distributions  
172 are re-shuffled, with potentially far-reaching consequences for ecosystems functioning<sup>3,7,32,33</sup>.

173 Our results further highlight that loss of individuals can occur simultaneously with increases  
174 in richness, emphasizing that temperature-related changes in richness and abundance can be  
175 decoupled. Abundance declines may be occurring for more thermally restricted species,  
176 owing to reduced performance and population declines, as critical thermal thresholds are  
177 crossed<sup>4-6</sup>, for instance related to the adverse effects of increasing temperatures on metabolic  
178 rates and primary production<sup>29,34</sup>. Influxes of climate immigrants can also drive local declines  
179 in populations due to greater grazing and predation rates<sup>35,36</sup>. The abundance declines across  
180 our warmest temperate locations in the ocean suggest warming-related destabilization of  
181 populations possibly reflecting reductions in the carrying capacity of marine ecosystems.

182 We also find strong interacting effects of the baseline climate on both abundance and richness  
183 change in the ocean, which responded in different directions in our warmest temperate  
184 locations. This highlights that rising temperatures in locations that are already warm can lead  
185 to greater assemblage restructuring. Our findings may reflect the patchiness in temperature  
186 regimes across similar latitudes, for example due to altitudinal or depth gradients, proximity  
187 to the coast, or ocean currents, and may explain why latitude is a poor predictor for  
188 assemblage-level changes in our analysis. Specifically, within the scope of our data, baseline  
189 climate better captured context-dependent spatial patterns, and allowed us to detect  
190 biodiversity change across pockets of warmer and colder areas within latitudinal bands.

191 Baseline climate therefore emerges as a major predictor of temperature-related biodiversity  
192 change in marine systems, as recently also found by others<sup>14,18</sup>. Specifically, marine species  
193 track isotherms more readily in initially warm waters<sup>14</sup>, which may be due to tropical species



194 overall living closer to their upper thermal limits, and thus more promptly responding to  
195 warming trends.

196 Overall, and despite faster warming on land, we did not detect systematic responses in  
197 richness or abundance with temperature change for terrestrial assemblages. The stronger  
198 responses observed for marine assemblages are consistent with reported faster range shifts in  
199 the ocean and higher sensitivity of marine organisms to temperature change compared to  
200 terrestrial species<sup>3,12,14–16</sup>. Our findings are also consistent with warming-related local  
201 extirpations being twice as common in the ocean as on land<sup>15</sup>. The lack of systematic  
202 assemblage-level change associated with temperature change on land might be due to greater  
203 thermoregulation capacity and wider thermal safety margins of terrestrial taxa<sup>8,15,16</sup>.

204 Additionally, compared to seascapes, higher landscape complexity enables terrestrial species  
205 to exploit thermal microhabitats, thus allowing for the persistence of local populations for  
206 longer periods<sup>8,20</sup>. Indeed, access to thermal refugia was reported to be a fundamental factor  
207 underlying the relatively low vulnerability of terrestrial ectotherms to warming, and  
208 emphasizes the potential deleterious combined effects of warming and land-use changes<sup>15</sup>.

209 Finally, a weaker link between assemblage responses and temperature change on land may be  
210 due to other factors, such as land-use change and moisture availability, posing stronger  
211 constraints on local biodiversity. Nonetheless, the smaller magnitude or slower responses of  
212 terrestrial species to temperature change<sup>11,12,15,24,37,38</sup>, combined with the faster rates of  
213 warming on land, indicate a potentially higher accumulation of climatic debt (i.e. response  
214 lags) among terrestrial *versus* marine taxa<sup>3,12,14,19,37,39–41</sup>. Additional research with higher-  
215 resolution temperature data matching the scale of organisms' responses is needed to better  
216 quantify terrestrial assemblages' responses to temperature change, and these developments  
217 remain a major challenge for many different taxa.

218 Our results warrant discussing some caveats. First, as commonly noted for biodiversity data,  
219 both taxonomic and geographic biases exist<sup>23,42</sup>, with the majority of our data coming from  
220 the Northern Hemisphere, and disproportionately representing marine fish and terrestrial  
221 birds. Yet, we did not detect systematic differences in responses among the taxonomic groups  
222 in our data. Additionally, our ability to detect systematic trends on land may have been  
223 affected by the smaller number of terrestrial studies analysed, as illustrated by credible  
224 intervals often overlapping zero when using smaller subsets of marine data to estimate  
225 biodiversity change. The apparent inconsistency between our results and previous range shifts  
226 studies on land can be further reconciled by the different ecological levels at which such  
227 changes are being evaluated. As marine species track changing isotherms more closely than  
228 terrestrial species<sup>14</sup>, range shifts are more immediately translated at the assemblage-level in  
229 the ocean. On land, systematic effects on richness and abundance can be harder to detect  
230 given the general higher thermal tolerance and slower responses of terrestrial species.

231 Our analyses represent a first step towards explaining divergent patterns of assemblage-level  
232 biodiversity change across the planet<sup>24,43</sup>. Overall, our results provide strong support for the  
233 expectation that divergent biodiversity trajectories may arise as a consequence of global  
234 warming, with polar and temperate regions likely acting as “sinks”, and tropical regions as  
235 “sources”<sup>5,7,32</sup>. In turn, these responses could prompt a shift in the latitudinal diversity  
236 gradient towards higher latitudes, with faster rates of change in the ocean. While we focused  
237 here on temperate regions, tropical and polar biomes are predicted to undergo severe  
238 restructuring in response to temperature change, albeit along different trajectories<sup>5,7,12</sup>.

239 However, lack of sufficient biodiversity monitoring data for tropical and polar systems<sup>23,42</sup>  
240 hampers a comprehensive assessment of assemblage-level responses to temperature change in  
241 these regions, which remains a key challenge for further research.

242 Future global warming impacts on biodiversity are likely to exceed and potentially diverge  
243 from the changes revealed here<sup>7,32,34,44–46</sup>. Indeed, initial increases in richness and abundance  
244 in response to warming may be followed by losses if warming continues<sup>6,47,48</sup>. Declines in  
245 marine systems may affect food security and livelihoods of human populations that depend  
246 on the ocean<sup>6,49</sup>. Additionally, while a consistent signal of temperature change was not  
247 evident on land, future impacts on terrestrial assemblages are expected from continuing rising  
248 temperatures, extreme heat events, fires, and lack of moisture<sup>34,45,50</sup>. Because the Earth is  
249 committed to further warming, a systematic reduction of greenhouse gas emissions alongside  
250 efforts to further prevent habitat loss and improve habitat connectivity will be fundamental to  
251 allow species to track suitable climates across increasingly impacted land- and seascapes and  
252 to avoid severe biodiversity disruption and loss.

253

## 254 **Methods**

### 255 Biodiversity data and trends

256 BioTIME<sup>23</sup> is currently the largest global database of assemblage time series, including 386  
257 individual studies (Study ID; plus extended data sources) across different taxonomic groups,  
258 holding over 12 million records of abundance for over 45,000 species. For this analysis, we  
259 only included studies reporting counts of individuals per species in terrestrial and marine  
260 systems. We excluded freshwater studies as these are too few to confidently analyse  
261 biodiversity trends across taxa and different regions.

262 Each study is comprised of distinct samples (i.e. individual plots, transects, tows, etc.  
263 sampled at a given time), and the number of samples can vary among years within each  
264 study. As the spatial extent varies among studies, we gridded those studies that had large  
265 extents and multiple sampling locations into hexagonal cells of  $\sim 96\text{km}^2$ ; many studies were  
266 not partitioned because they were contained within a single cell<sup>24</sup>. Specifically, each sample  
267 was assigned to different combinations of study ID and grid cell based on its latitude and  
268 longitude, resulting in new assemblage time series (each with multiple samples across years).  
269 These new time series were given a unique identifier that was the concatenation of the study  
270 ID and the grid cell reference number, and thus contained samples from only one study – i.e.  
271 the integrity of each study and each sample was maintained. This process allowed us to relate  
272 biodiversity and temperature trends at a standardized resolution. To minimise the effect of  
273 unobserved species on estimates of biodiversity change, we calculated the abundance-based  
274 coverage<sup>51</sup> of each annual sample within each time series, and removed all samples with  
275 coverage less than 0.85. To be able to reliably estimate biodiversity trends, we restricted our  
276 analysis to time series sampled in at least five years (not necessarily consecutive). Because  
277 the number of samples can vary among years, we used sample-based rarefaction<sup>25</sup> to  
278 standardise the number of samples among years for each time series before calculating the

279 biodiversity metrics. Specifically, we identified the minimum number of samples taken in  
280 each year within each assemblage time series; this minimum was then used to randomly  
281 sample each year down to that number of samples. Finally, given the paucity of data  
282 representing polar and tropical regions, we excluded these regions (based on absolute  
283 latitudinal cut-offs at 60° and 23.5°, respectively). This process yielded 21,500 assemblage  
284 time series representing 156 original studies (Fig. S1; Table S1) between 1900 and 2016,  
285 across 19,875 marine and 1,625 terrestrial locations. The average number of years sampled  
286 across the time series was 9.2 years, with the longest time series spanning 97 years (Fig. S2).

287 To quantify rates of biodiversity change, we calculated linear trends over time for species  
288 richness (logS), total abundance (logN), number of species gains and species losses. Counts  
289 of gains and losses retained species identity information, and were quantified based on  
290 comparison with the first year sampled in each time series. For losses, a positive slope means  
291 the number of species lost from a location is increasing through time; negative slopes  
292 represent time series where the magnitude in species losses decreased over time. We repeated  
293 the sample-based rarefaction process described above 199 times for each time series,  
294 recorded the values and took the median for each biodiversity metric in each year, in order to  
295 reduce the effect of any outlier samples on our estimates. We used ordinary least squares  
296 regression because we were interested in the long-term direction and magnitude of the  
297 biodiversity trends, and to allow us to compare the rates of change among locations, realms  
298 and metrics. We retained the estimated slope and standard error for each time series for use in  
299 our second-stage meta-analytical models.

300

301 Temperature data and trends

302 We focus on temperature as a climate variable because of its influence on every level of  
303 biological organization, from individual metabolic rates to biological communities' dynamics  
304 and structure<sup>29-31</sup>. We extracted temperature records from HadCRUT4<sup>26,27</sup>, specifically the  
305 HadSST3 data for marine Sea Surface Temperature (SST) on a 1° resolution, and the  
306 CRUTEM4 data for air temperature on land on a 0.5° resolution. We did not harmonize the  
307 spatial resolution between the two data sources because we wanted to use the best available  
308 data in each realm. For the location of each biodiversity time series, we extracted monthly  
309 mean temperature records for the duration of the biodiversity monitoring period  
310 ( $\text{Year}_{\text{start}}:\text{Year}_{\text{end}}$ ), and estimated mean temperature trends using generalized additive models  
311 (GAM), including a temporally autocorrelated error structure (package mgcv<sup>52</sup>). This also  
312 allowed us to assess if accounting for seasonality within years would improve model  
313 performance. We used AIC to compare models with and without “month”, selecting the best  
314 model for each time series. We extracted the linear slope from the model, which summarises  
315 the trend for mean annual temperature change.

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

322

## 323 Meta-analysis

324 Having estimated the trends for biodiversity and temperature independently for each individual  
325 time series, we assessed the effect of temperature change on the rates of change of each  
326 biodiversity metric in a second-stage analysis. We employed a meta-analytical Bayesian  
327 framework using the package brms<sup>56,57</sup> (version 2.6.0), and fitted generalized linear models to  
328 each realm separately, having initially evaluated that there was an effect of realm when fitting  
329 a full model. All models were created using the Stan computational framework ([http://mc-](http://mc-stan.org/)  
330 [stan.org/](http://mc-stan.org/)) accessed via brms. To determine whether the baseline climate modulated the  
331 biodiversity responses, models were fit with an interaction term between temperature change  
332 and the long-term average temperature at each location. Additionally, we fitted similar models  
333 using latitude. We used two random effect terms: one allowing for different slopes per  
334 taxonomic group (Taxon), and another allowing for different intercepts per study ID nested  
335 within Taxon. This allowed us to account for: 1) potentially different responses to temperature  
336 change among taxa; 2) differences in species richness among taxa, as well as different  
337 assemblage time series originating from the same study, and different studies monitoring the  
338 same taxonomic groups across the BioTIME database, respectively; and 3) spatial  
339 autocorrelation. The different taxonomic groups were informed by the original data sources  
340 metadata, and were: "Amphibians", "Benthos", "Birds", "Fish", "Mammals", "Marine  
341 invertebrates", "Terrestrial invertebrates", "Terrestrial plants", and "Multiple taxa". "Multiple  
342 taxa" refers to Study IDs where the sampling methodology captured multiple taxa  
343 simultaneously. Additionally, taxonomic groups with only very few studies in BioTIME (e.g.  
344 reptiles) were included in this group for practical reasons; we note this category represented  
345 only 9% of the original studies and 5% of the standardised time series.

346

347 The overall model structure implemented for each realm was:

348  $\Delta \text{Biodiversity} \sim 0 + \Delta \text{Temperature} * \text{Long-term average temperature} +$   
349  $(0 + \Delta \text{Temperature} | \text{Taxon}) + (1 | \text{Taxon}/\text{StudyID}).$

350 The meta-analytical framework implemented allows the response variables to be weighted by  
351 their uncertainty; specifically we included the estimated standard errors for the biodiversity  
352 trends using the function `se()` when specifying the formula for the models, using the `brms`  
353 syntax<sup>56,57</sup>:  $\Delta \text{Biodiversity} | \text{se}(\Delta \text{Biodiversity}, \text{sigma} = \text{TRUE})$ . Additionally, a global intercept  
354 equal to zero was specified to reflect a scenario where there is no biodiversity change when  
355 all the independent variables are zero; i.e., the model assumes that no change in temperature  
356 would correspond to no change in the assemblage metrics for the average baseline climate  
357 (i.e. at the mean value across our data).

358

359 Models were run using four chains, each with 8,000 iterations, with a warm up of 4,000 and  
360 non-informative flat priors. Stan implements Hamiltonian Monte Carlo and its extension, the  
361 No-U-Turn Sampler (NUTS) algorithms, which converge quickly<sup>57</sup>. Convergence was  
362 assessed by visually examining trace plots and using Rhat values (the ratio of the effective  
363 sample size to the overall number of iterations, with values close to one indicating  
364 convergence)<sup>57</sup>. All the analyses were run in R version 4.3.1<sup>58</sup>.

365

366

367 Sensitivity analysis

368 To evaluate the robustness of potential interactions with the baseline climate, we additionally  
369 ran our models with two alternative baseline temperature variables. To that end, we extracted  
370 the variables “Mean Temperature of Warmest Quarter” from WorldClim and “Long-term  
371 maximum sea surface temperature” from Bio-ORACLE, as well as the average temperature



372 in the first year sampled for each biodiversity time series from the same dataset that was used  
373 to quantify the trends (i.e. the spatially less resolved HadCRUT4 dataset).

374 To evaluate whether uneven sampling could be driving the observed differences between the  
375 marine and terrestrial realms, we fitted models to subsets of the marine data that matched  
376 both the number of locations (1,625 time series) and the latitudinal range of the terrestrial  
377 data. We did not attempt to control for temperature change differences between realms  
378 because this is part of the signal to be modelled. We fitted the meta-analytical models to 100  
379 random subsamples for each biodiversity metric, illustrating that the estimates for the marine  
380 realm are robust (Fig. S5). This analysis also illustrated that a smaller sample size may have  
381 affected our ability to detect systematic biodiversity changes on land, given that confidence  
382 intervals overlapping zero occurred for several of the meta-analytical models fit to subsets of  
383 the marine data matching the number of terrestrial time series. We further evaluated that  
384 biodiversity responses did not show any clear pattern as a function of the number of years  
385 sampled, duration and start year of the time series. Although shorter time series tend to show  
386 higher rates of biodiversity change, these also tend to have higher standard errors, which are  
387 in turn accounted for within the meta-analytical framework. We further note there were no  
388 notable differences in the estimated rates of biodiversity change as a function of number of  
389 sampled years between marine and terrestrial time series. Thus, we believe the temporal  
390 heterogeneity of sampling in our data is very unlikely to drive our findings (Figs. S6 and S7).

391

392 **Author contributions**

393 M.D. and A.M.S. conceived the idea, and all authors contributed to design the project. L.H.A.  
394 analysed the data in close consultation with S.A.B., A.E.B., M.D. and A.M.S.. L.H.A. wrote  
395 the first draft of the manuscript. L.H.A., A.E.B., M.D., A.M.S., S.A.B., C.W., S.R.S. and  
396 A.E.M. all contributed to manuscript completion and revision. M.D. and A.M.S. are shared  
397 senior authors.

398

399

400 **Data Availability**

401 All the data can be accessed through the BioTIME database on Zenodo  
402 (<https://doi.org/10.5281/zenodo.1211105>) or through the BioTIME website ([http://biotime.st-](http://biotime.st-andrews.ac.uk/)  
403 [andrews.ac.uk/](http://biotime.st-andrews.ac.uk/)).

404

405

406 **Code Availability**

407 Code to reproduce the analysis is available on GitHub  
408 ([https://github.com/lauraantao/Temp\\_Biodiv\\_Change](https://github.com/lauraantao/Temp_Biodiv_Change)) and in an online archive at Zenodo<sup>59</sup>.

409

410

411 **Competing interests**

412 The authors declare no conflict of interest.

413

414

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- 574

575 **Figure Legends**

576

577 **Figure 1. Conceptual figure of the mechanisms underlying our hypotheses for how**  
578 **temperature-related biodiversity change may unfold unevenly across the planet,**  
579 stemming from the (a) latitudinal gradients in species diversity (decrease with latitude) and  
580 species thermal tolerances breadths or thermal safety margins (TSM; increase with latitude);  
581 and (b) differences between marine and terrestrial realms in terms of environmental  
582 heterogeneity and geographical range shifts. Note this is a schematic simplified  
583 representation of these large-scale mechanisms and patterns (for instance, TSMs are not  
584 necessarily linear with latitude<sup>15</sup>, and heat tolerance declines more steeply with latitude for  
585 marine ectotherms<sup>60</sup>).

586

587 **Figure 2. Variation in temperature and local biodiversity trends across the time series**  
588 (marine in blue, n= 19,875; terrestrial in green, n= 1,625). **(a)** Each dot indicates the rate of  
589 temperature change ( $^{\circ}\text{C year}^{-1}$ ) for a specific time series, coloured according to the long-term  
590 average temperature. There was no clear latitudinal pattern in temperature change: while the  
591 majority of locations in both realms experienced warming, and more so for terrestrial  
592 locations **(b)**, many locations underwent cooling during the period examined. Local  
593 biodiversity change estimates (rate  $\text{year}^{-1}$ ) also exhibited wide variability **(c)** (note the  
594 different scales for the different metrics; x-axes were truncated to improve clarity). Tick  
595 dashed vertical lines indicate the overall mean per realm in all the density plots. The  
596 biodiversity time series locations cover numerous habitats and biomes, and sample a large  
597 range of the planet's long-term average temperature gradient (although most data originate  
598 from the Northern Hemisphere; Fig. S1).

599

600 **Figure 3. Biodiversity responses to temperature change and its interaction with long-**  
601 **term average temperature (i.e. baseline climate).** Marine locations (blue) exhibited  
602 stronger responses compared to terrestrial locations (green), while baseline climate  
603 modulated these responses in divergent directions. The main effects of baseline climate were  
604 negligible, and are not shown. Bars represent the estimated parameters and whiskers indicate  
605 the 95% credible intervals from the Bayesian meta-analysis (note the different scales for the  
606 different metrics); estimated parameters were considered to represent signals in the responses  
607 when the credible intervals did not include zero (Table S2; see Tables S3-S6 for complete  
608 model outputs).

609

610 **Figure 4. Biodiversity responses to the combined effect of temperature change and**  
611 **baseline climate.** Each panel depicts the rate and direction of biodiversity change depending  
612 on the temperature change experienced (cooling *versus* warming) and on the long-term  
613 average temperature (colder *versus* warmer), where red indicates positive slopes for the  
614 biodiversity response, and blue indicates negative slopes (note the different scales across the  
615 different metrics), for marine (top row) and terrestrial realms (bottom row). Grey dots  
616 represent the distribution of data along the two axes. Stars indicate when the 95% credible  
617 intervals for the interaction term from the meta-analytical models did not overlap zero (Fig. 3,  
618 Table S2).

619

Figure 1

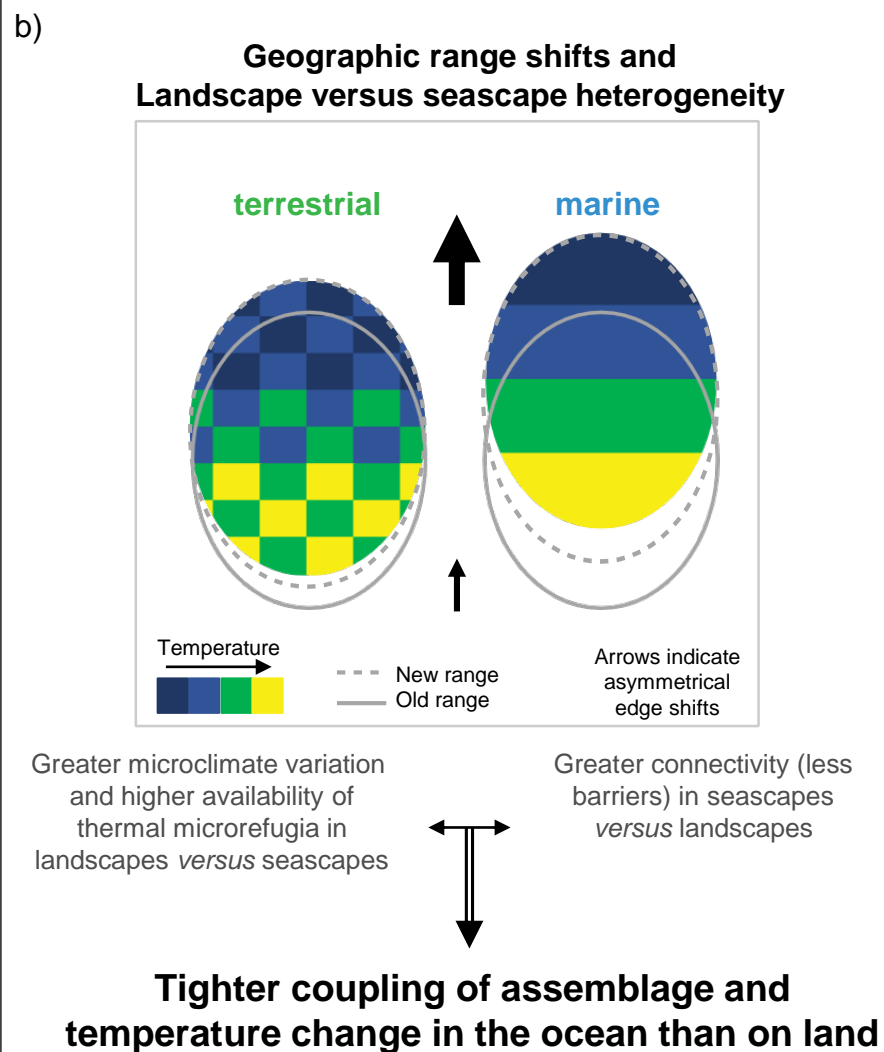
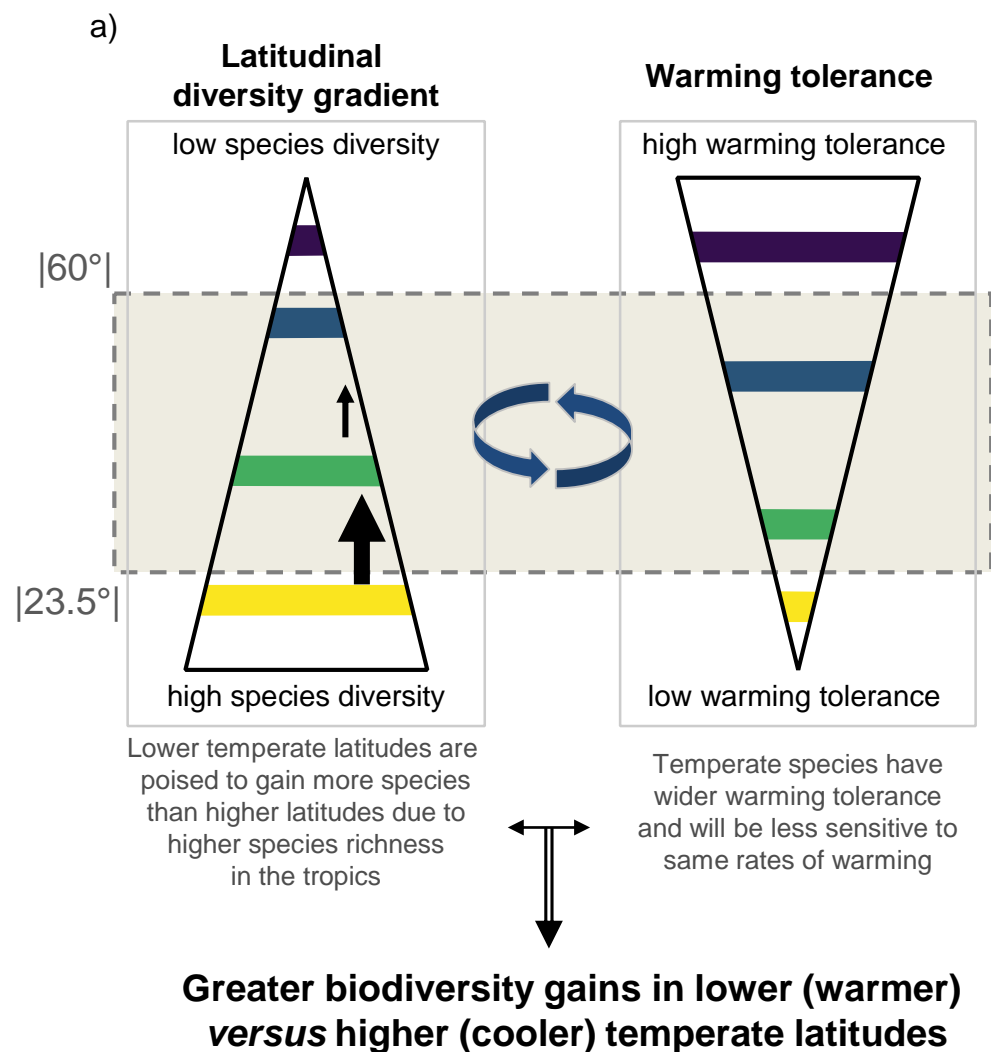


Figure 2

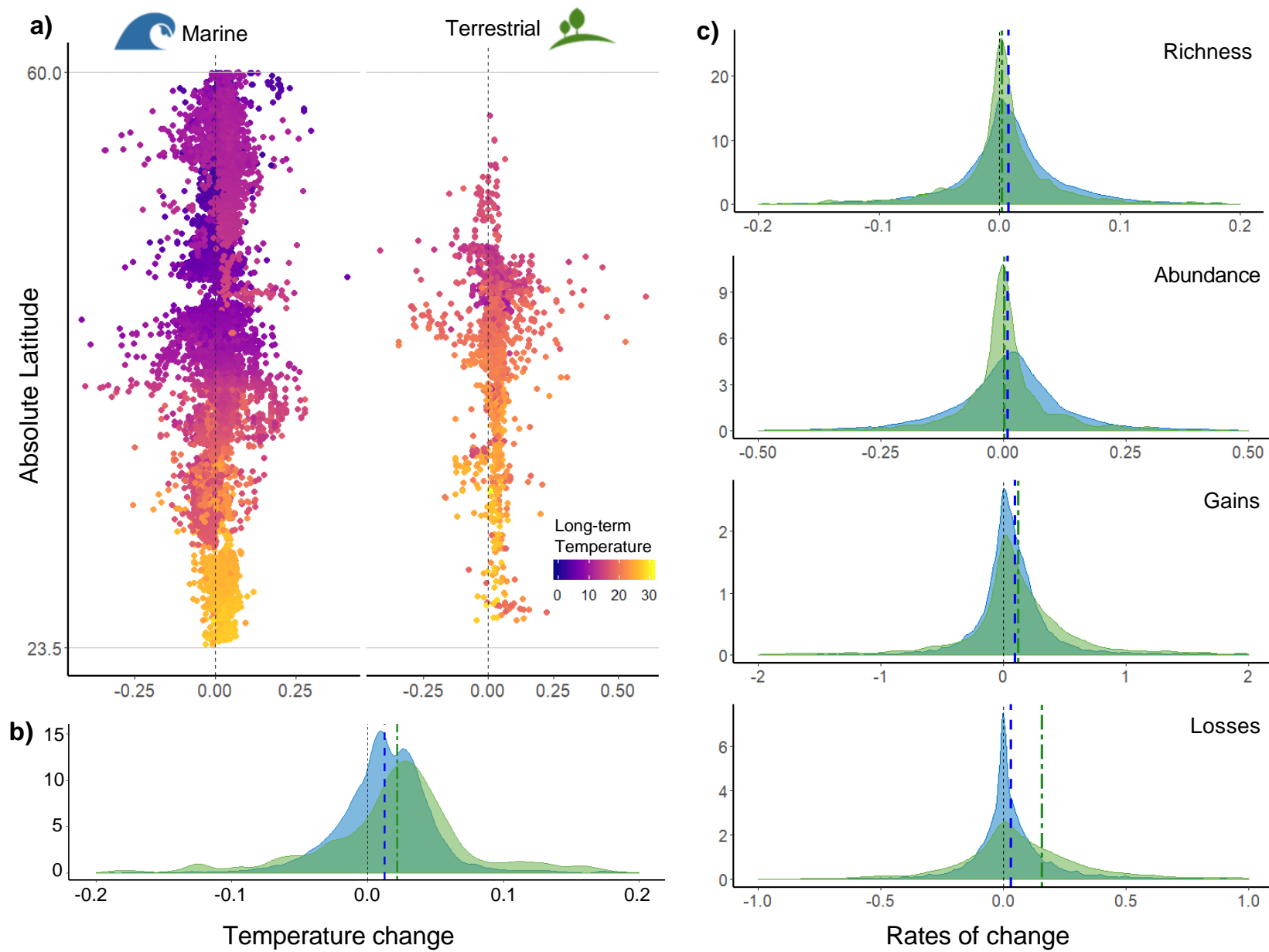


Figure 3

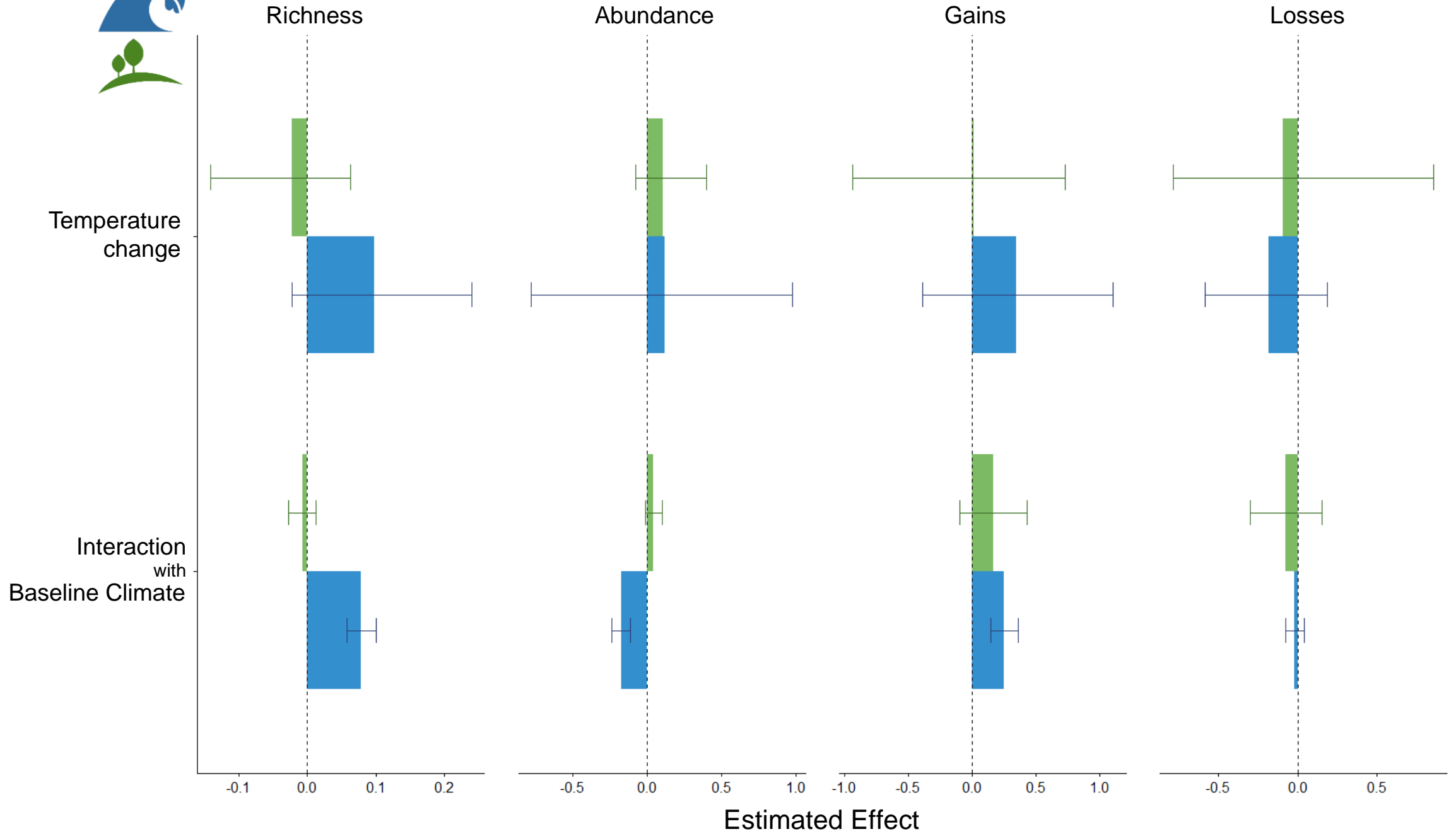


Figure 4

