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Temperature-related biodiversity change across temperate marine and terrestrial systems

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

Climate change is driving a reorganization of ecological communities as species track changes in air and ocean temperatures[1–3]. However, global warming is not unfolding evenly across the planet, and this heterogeneity is layered over the uneven distribution of biodiversity. Populations of thermally restricted species may decline with warming as individuals die, fail to reproduce or move to more suitable locations[4–6]. Indeed, declines are typically expected for tropical species, since they have narrower thermal tolerances than temperate species and live closer to their upper thermal limits[5,7–10]. In contrast, species benefiting from warming may exhibit abundance increases and expand their geographic ranges[1–4,11]. Thus, mid- to high-latitudes undergoing warming may provide suitable habitat for species expanding their ranges poleward[4,12]. Because the tropics hold the majority of the world's species[13], lower-latitude warming temperate regions may experience larger increases in species richness and abundance compared to temperate locations at higher latitudes, due to a larger source pool of climate immigrants (Fig. 1). Biodiversity change may further depend on the baseline climate—that is, within latitudinal bands the effects of warming might differ between initially warmer versus colder regions[3,5,12,14]. For instance, warmer temperate regions may offer greater habitat suitability for climate immigrants from lower latitudes.

Warming-induced biodiversity change may also be stronger in the ocean than on land[3,15,16]. Marine species are highly responsive to temperature change and can track changing isotherms with fewer barriers to dispersal, compared to terrestrial species[3,14–19]. Moreover, the availability of thermal microrefugia is limited in the ocean, while in terrestrial ecosystems organisms can seek shade or burrow in soil to buffer the effects of warming[17,20] (Fig. 1). Therefore, biodiversity responses to temperature change are expected to be more immediate and directly

detectable for marine ecosystems; this expectation is supported by a growing literature which has quantitatively compared individual species' responses to temperature change between marine and terrestrial realms[3,14–16]. However, the net effects of temperature-related species' movements and abundance changes on assemblage-level diversity have not yet been systematically investigated across realms.

Here, we quantify temperature-related species richness and total abundance change in marine and terrestrial assemblages across temperate regions of the planet (23.5–60.0° absolute latitude; Extended Data Fig. 1). Specifically, we test two predictions for the effects of temperature change on assemblage-level diversity: (1) species richness and total abundance will increase with warming, and such increases will be greatest across relatively warm regions that border the species-rich tropics; and (2) the coupling of assemblage and temperature change will be tighter in the ocean than on land. These predictions are informed by the interaction between the latitudinal gradients in species richness and warming tolerance, and by the differences between realms regarding environmental heterogeneity and species distribution shifts (Fig. 1).

We focus on local assemblage-level trends, rather than species-specific responses, and quantify changes in both total abundance and species richness. These two metrics can be decoupled from each other, and abundance is typically more responsive to environmental change than richness[21,22]. We further disentangle richness change into species gains and losses to better understand the underlying dynamics of temperature-related biodiversity change. To test our expectations, we used the largest database of assemblage time series, BioTIME[23], which includes studies of plants, invertebrates, birds, mammals and fish. These assemblages consist of co-occurring species systematically sampled through time. Since
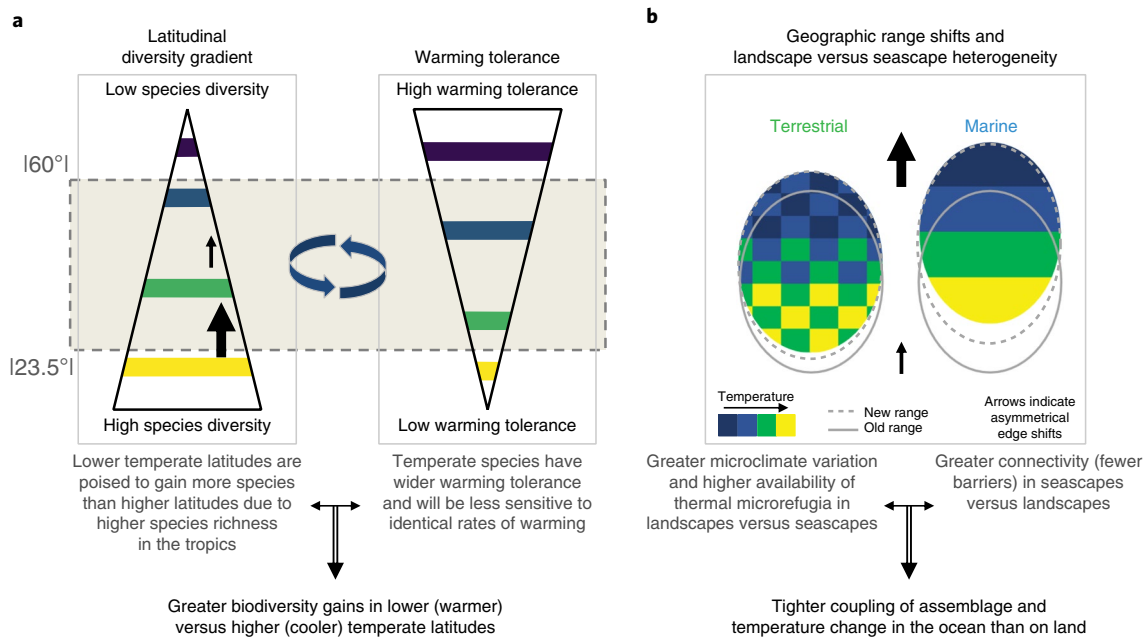
Fig. 1 | Conceptual figure of the mechanisms underlying our hypotheses for how temperature-related biodiversity change may unfold unevenly across the planet. a,b, These stem from the latitudinal gradients in species diversity (decrease with latitude) and species thermal tolerance breadths or thermal safety margins (increase with latitude) (**a**); and differences between marine and terrestrial realms in terms of environmental heterogeneity and geographical range shifts (**b**). Note that this is a schematic simplified representation of these large-scale mechanisms and patterns (for instance, thermal safety margins are not necessarily linear with latitude[15] and heat tolerance declines more steeply with latitude for marine ectotherms[60]).

spatial extent varies among studies in BioTIME, we harmonized the biodiversity observations to a common spatial resolution to minimize the influence of variation in spatial extent on our results[24]; this allowed us to quantify the effect of temperature change at a standardized resolution across regions and realms. We first estimated trends in biodiversity and temperature separately, and then quantified the relationships between the two.

Specifically, for each study we allocated individual samples to 96-km² hexagonal grid cells based on their location (see Methods;[24]); that is, each sample was assigned to a specific combination of study ID and grid cell based on its latitude and longitude, resulting in equal-extent assemblage time series with multiple samples across years. Because each time series contained samples from only one study, the integrity of sampling methods within each study was maintained. We used these spatially harmonized assemblage time series in our analysis, selecting data from temperate regions only (since these are the better sampled regions within BioTIME). We then selected time series with at least 5 years of sampling (mean = 9.2 years), yielding 21,500 assemblage time series across both realms (19,875 marine and 1,625 terrestrial from 156 original studies; Extended Data Figs. 1 and 2 and Supplementary Table 1). Because the number of samples can vary from year to year within each time series, we used sample-based rarefaction[25] to equalize sampling effort among years and then quantified trends in richness, total abundance and number of species gained or lost. For the same locations and for the time spans matching the duration of the biodiversity monitoring periods, we extracted mean monthly temperature records from HadCRUT4[26,27] and estimated the corresponding annual rates of sea surface or air temperature change. We then quantified the relationships between changes in biodiversity and changes in temperature with meta-analytical Bayesian hierarchical models, allowing responses to vary among taxonomic groups. To test our expectations, we included an interaction term between temperature change and long-term average temperature (that is, baseline climate) or latitude in our models, fitted separately for the marine and terrestrial realms.

Results

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

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

Our analysis highlights the fundamental role of climate baselines in modulating biodiversity responses in the ocean, given that latitude showed no or very weak interacting effects with temperature change (Extended Data Fig. 4). Further tests revealed only a weak correlation between either baseline climate or latitude and temperature change (Spearman's rank correlation, $\rho = 0.063$ and 0.098, respectively). As such, the correlation structure of our covariates is unlikely to bias our results towards a positive effect of temperature change when combined with baseline climate rather than latitude.
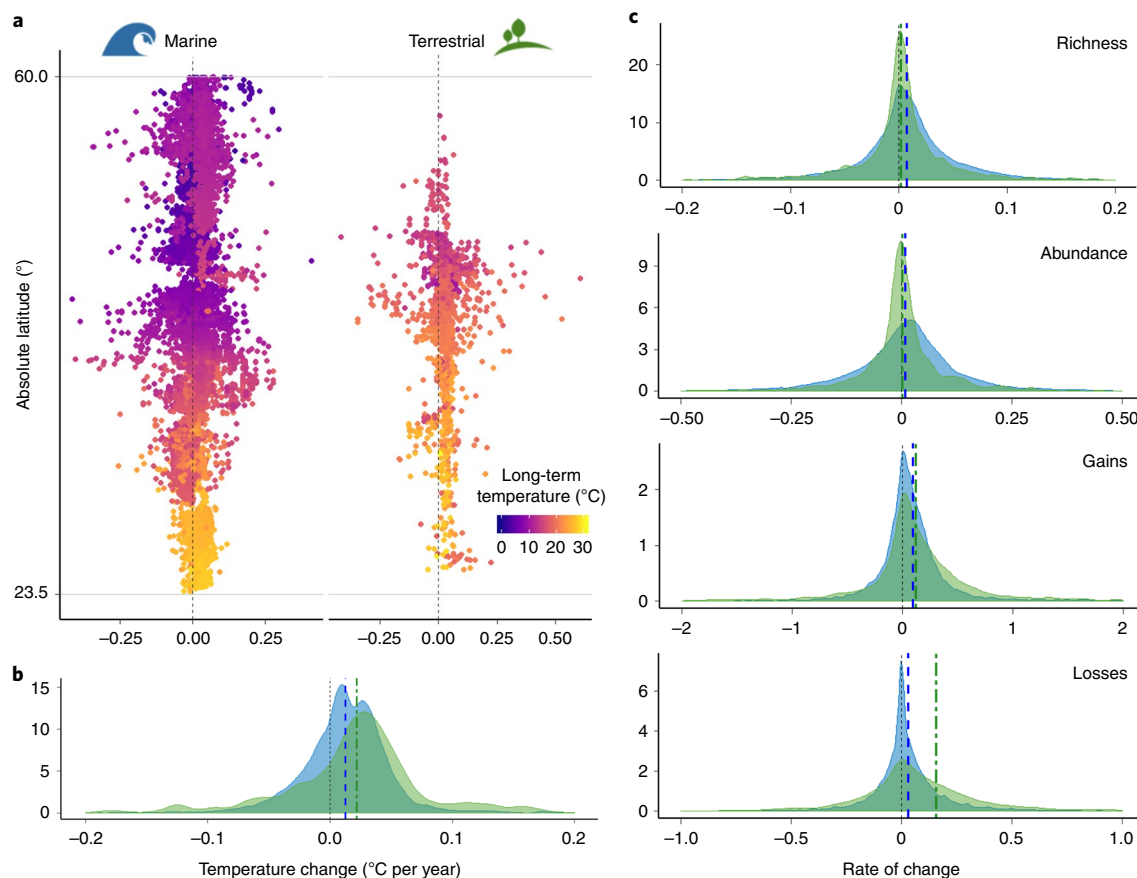
Fig. 2 | Variation in temperature and local biodiversity trends across the time series. a, Each dot indicates the rate of temperature change (°C per year) for a specific time series, coloured according to the long-term average temperature. There was no clear latitudinal pattern in temperature change: while the majority of locations in both realms experienced warming, and more so for terrestrial locations (**b**), many locations underwent cooling during the period examined. Local biodiversity change estimates (rate per year) also exhibited wide variability (**c**) (note the different scales for the different metrics; x axes were truncated to improve clarity). Blue denotes marine (n=19,875) and green indicates terrestrial (n=1,625). Coloured dashed vertical lines indicate the overall mean per realm in all density plots and black lines indicate zero. The biodiversity time series locations cover numerous habitats and biomes, and sample a large range of the planet's long-term average temperature gradient (although most data originate from the Northern Hemisphere; Extended Data Fig. 1). Credit: b farias, CL (wave image) and Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/).

Our results were highly robust to a number of further sensitivity tests addressing biases in the BioTIME dataset, differences amongst covariates and model structure. We found similar responses in the marine realm when using subsets of the marine data that match the number of locations and latitudinal range of the terrestrial data, despite increased uncertainty in model estimates (Extended Data Fig. 5). Our results were consistent across different baseline temperature variables (long-term annual and maximum temperature, and annual mean temperature of the first year) and between different temperature databases for quantification of climate baselines (Extended Data Fig. 4; see Methods). Additionally, we did not detect any systematic effect of the number of years sampled, temporal duration or start year of the time series on the estimated rates of biodiversity change (Extended Data Figs. 6 and 7). Finally, there was no evidence for systematic differences in biodiversity responses among the different taxonomic groups (as estimated via the random slope model components; Extended Data Figs. 8 and 9; complete model outputs with posterior estimates are shown in Supplementary Tables 3–6).

Discussion

We reveal striking differences in warming-related biodiversity change between marine and terrestrial realms across temperate regions, with a much stronger signature of warming on marine assemblages. Our results are unlikely to be due to confounding factors, given that climate

change is poorly spatially correlated with other anthropogenic drivers of change for both marine and terrestrial realms[28]. Furthermore, temperature is expected to be a strong driver of biodiversity change given its fundamental role in biological processes[29–31].

The warming-related increase in local marine species richness is consistent with the expectation that as the Earth's climate warms, temperate regions undergoing warming will receive an influx of species tracking suitable temperatures, and increases in warm-affinity generalists[2,6,7,18,29]. This warming-related increase in species richness is probably, in part, underpinned by species from lower latitudes shifting their ranges poleward to avoid exceeding their upper thermal limits[4,12,14]. Indeed, projected rates of extirpation in response to recent and future warming are highest for tropical marine species[7,32], which in turn are better able to track changing isotherms[14]. Here, we find that species gains outpaced losses in the warmest temperate locations in the ocean where temperature has also increased. This finding is consistent with asymmetrical responses between species range edges, with faster colonizations expected following climatic niche expansion, and with slower extirpations linked to delayed responses at species' trailing edges[3,4]. The prevailing influx of species with warming is likely to lead to novel biotic communities and interactions as species distributions are reshuffled, with potentially far-reaching consequences for ecosystems' functioning[3,7,32,33].
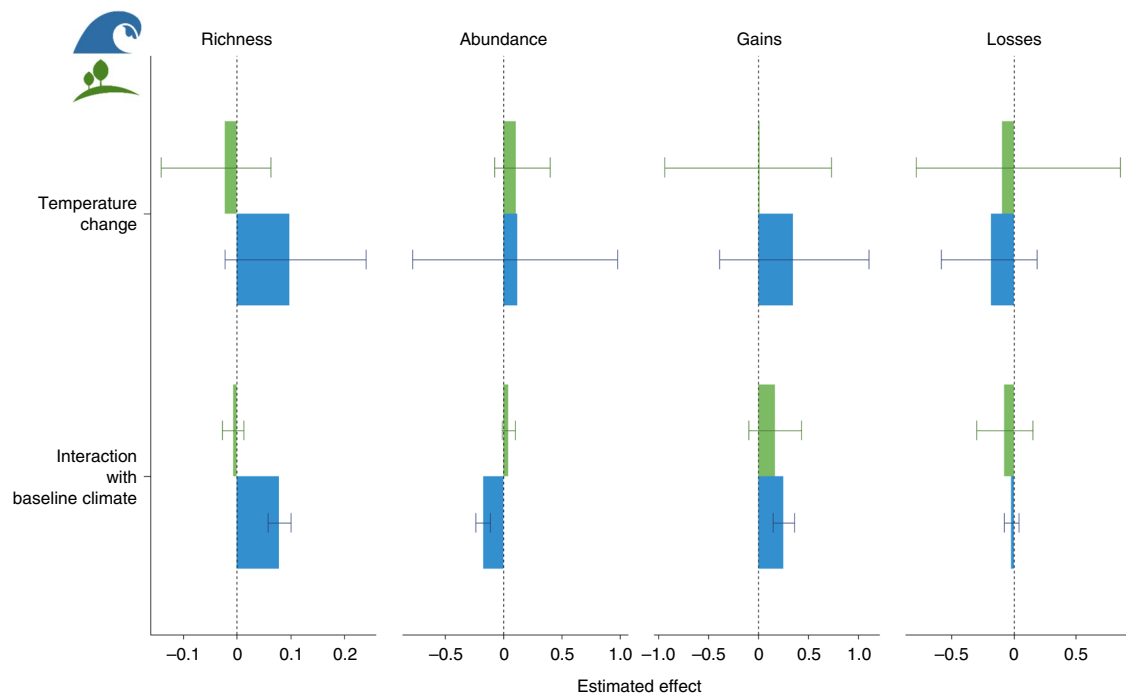
Fig. 3 | Biodiversity responses to temperature change and its interaction with baseline climate. Marine locations (blue) exhibited stronger responses compared to terrestrial locations (green), while baseline climate (that is, long-term average temperature) modulated these responses in divergent directions. The main effects of baseline climate were negligible, and are not shown. Bars represent the estimated parameters and whiskers indicate the 95% credible intervals from the Bayesian meta-analysis (note the different scales for the different metrics); estimated parameters were considered to represent signals in the responses when the credible intervals did not include zero (Supplementary Table 2; see Supplementary Tables 3–6 for complete model outputs). Credit: b farias, CL (wave image) and Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/).
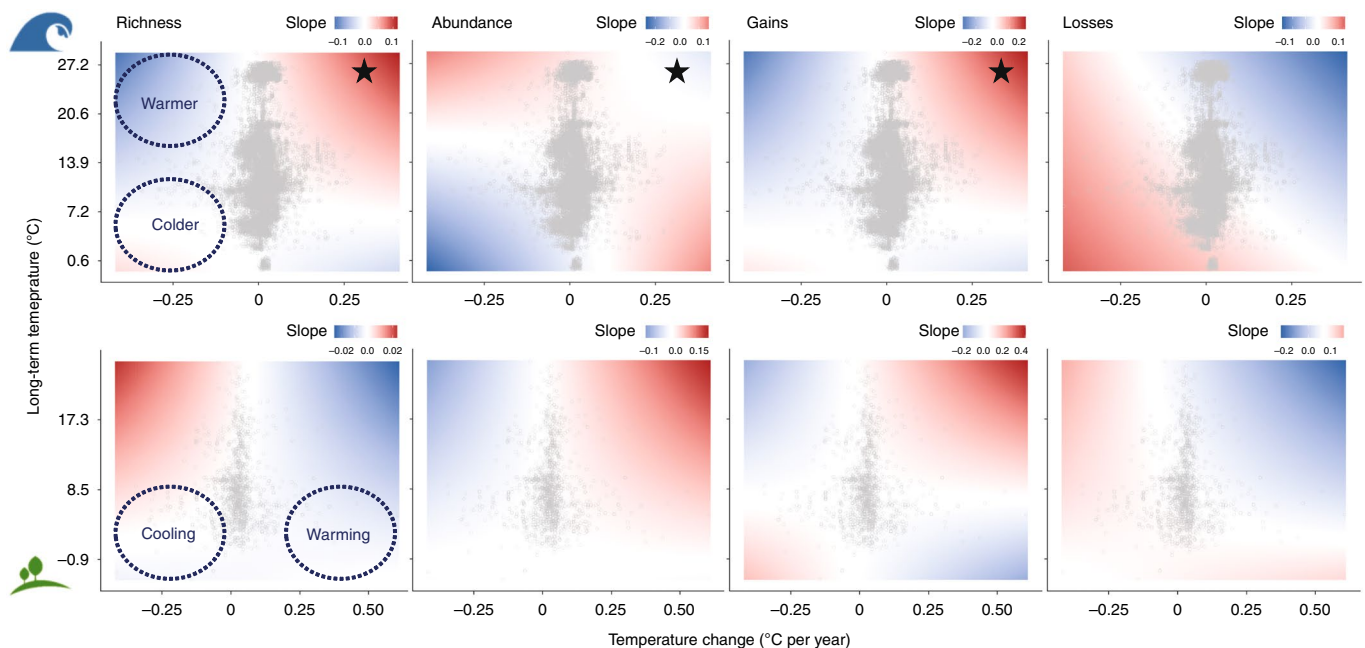

Fig. 4 | Biodiversity responses to the combined effect of temperature change and baseline climate. Each panel depicts the rate and direction of biodiversity change depending on the temperature change experienced (cooling versus warming) and on the long-term average temperature (colder versus warmer), where red indicates positive slopes for the biodiversity response and blue indicates negative slopes (note the different scales across the different metrics), for marine (top row) and terrestrial realms (bottom row). Grey dots represent the distribution of data along the two axes. Stars indicate when the 95% credible intervals for the interaction term from the meta-analytical models did not overlap zero (Fig. 3 and Supplementary Table 2). Credit: b farias, CL (wave image) and Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/).

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

We also find strong interacting effects of the baseline climate with temperature change on both abundance and richness change in the ocean, which responded in different directions in our warmest temperate locations. This highlights that rising temperatures in locations that are already warm can lead to greater assemblage restructuring. Our findings may reflect the patchiness in temperature regimes across similar latitudes—for example, due to altitudinal or depth gradients, proximity to the coast or ocean currents, and may explain why latitude is a poor predictor for assemblage-level changes in our analysis. Specifically, within the scope of our data, baseline climate better captured context-dependent spatial patterns and allowed us to detect biodiversity change across pockets of warmer and colder areas within latitudinal bands. Baseline climate therefore emerges as a major predictor of temperature-related biodiversity change in marine systems, as recently also found by others[14,18]. Specifically, marine species track isotherms more readily in initially warm waters[14], which may be due to tropical species overall living closer to their upper thermal limits, and thus more promptly responding to warming trends.

Overall, and despite faster warming on land, we did not detect systematic responses in richness or abundance with temperature change for terrestrial assemblages. The stronger responses observed for marine assemblages are consistent with reported faster range shifts in the ocean and higher sensitivity of marine organisms to temperature change compared to terrestrial species[3,12,14–16]. Our findings are also consistent with warming-related local extirpations being twice as common in the ocean as on land[15]. The lack of systematic assemblage-level change associated with temperature change on land might be due to greater thermoregulation capacity and wider thermal safety margins of terrestrial taxa[8,15,16]. Additionally, compared to seascapes, higher landscape complexity enables terrestrial species to exploit thermal microhabitats, thus allowing for the persistence of local populations for longer periods[8,20]. Indeed, access to thermal refugia was reported to be a fundamental factor underlying the relatively low vulnerability of terrestrial ectotherms to warming, and emphasizes the potential deleterious combined effects of warming and land-use changes[15]. Finally, a weaker link between assemblage responses and temperature change on land may be due to other factors, such as land-use change and moisture availability, posing stronger constraints on local biodiversity. Nonetheless, the smaller magnitude or slower responses of terrestrial species to temperature change[11,12,15,24,37,38], combined with the faster rates of warming on land, indicate a potentially higher accumulation of climatic debt (that is, response lags) among terrestrial versus marine taxa[3,12,14,19,37,39–41]. Additional research with higher-resolution temperature data matching the scale of organisms' responses is needed to better quantify terrestrial assemblages' responses to temperature change, and these developments remain a major challenge for many different taxa.

Our results warrant discussing some caveats. First, as commonly noted for biodiversity data, both taxonomic and geographic biases exist[23,42], with the majority of our data coming from the Northern Hemisphere and disproportionately representing marine fish and terrestrial birds. Nevertheless, we did not detect systematic differences in responses among the taxonomic groups in our data.

Additionally, our ability to detect systematic trends on land may have been affected by the smaller number of terrestrial studies analysed, as illustrated by credible intervals often overlapping zero when using smaller subsets of marine data to estimate biodiversity change. The apparent inconsistency between our results and previous range shifts studies on land can be further reconciled by the different ecological levels at which such changes are being evaluated. As marine species track changing isotherms more closely than terrestrial species[14], range shifts are more immediately translated at the assemblage-level in the ocean. On land, systematic effects on richness and abundance can be harder to detect given the general higher thermal tolerance and slower responses of terrestrial species.

Our analyses represent a first step towards explaining divergent patterns of assemblage-level biodiversity change across the planet[24,43]. Overall, our results provide strong support for the expectation that divergent biodiversity trajectories may arise as a consequence of global warming, with polar and temperate regions probably acting as 'sinks' and tropical regions as 'sources'[5,7,32]. In turn, these responses could prompt a shift in the latitudinal diversity gradient towards higher latitudes, with faster rates of change in the ocean. While we focused here on temperate regions, tropical and polar biomes are predicted to undergo severe restructuring in response to temperature change, albeit along different trajectories[5,7,12]. However, lack of sufficient biodiversity monitoring data for tropical and polar systems[23,42] hampers a comprehensive assessment of assemblage-level responses to temperature change in these regions, which remains a key challenge for further research.

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

Methods

Biodiversity data and trends. BioTIME[23] is currently the largest global database of assemblage time series, including 386 individual studies (study ID; plus extended data sources) across different taxonomic groups, holding >12 million records of abundance for >45,000 species. For this analysis, we included only those studies reporting counts of individuals per species in terrestrial and marine systems. We excluded freshwater studies because these are too few to confidently analyse biodiversity trends across taxa and different regions.

Each study is comprised of distinct samples (that is, individual plots, transects, tows and so on, sampled at a given time), and the number of samples can vary among years within each study. Because the spatial extent varies among studies, we gridded those studies that had large extents and multiple sampling locations into hexagonal cells of ~96 km²; many studies were not partitioned because they were contained within a single cell[24]. Specifically, each sample was assigned to different combinations of study ID and grid cell based on its latitude and longitude, resulting in new assemblage time series (each with multiple samples across years). These new time series were given a unique identifier that was the concatenation of the study ID and the grid cell reference number, and thus contained samples from only one study—that is, the integrity of each study and each sample was maintained. This process allowed us to relate biodiversity and temperature trends at a standardized resolution. To minimize the effect of unobserved species on estimates of biodiversity change, we calculated the abundance-based coverage[51] of each annual sample within each time series and removed all samples with coverage <0.85. To enable reliable estimation of biodiversity trends, we restricted our analysis to time series sampled in at least 5 years (not necessarily consecutive). Because the number of samples can vary among years, we used sample-based rarefaction[25] to standardize the number of samples among years for each time

series before calculating the biodiversity metrics. Specifically, we identified the minimum number of samples taken in each year within each assemblage time series; this minimum was then used to randomly sample each year down to that number of samples. Finally, given the paucity of data representing polar and tropical regions, we excluded these regions (based on absolute latitudinal cut-offs at 60° and 23.5°, respectively). This process yielded 21,500 assemblage time series representing 156 original studies (Extended Data Fig. 1 and Supplementary Table 1) between 1900 and 2016, across 19,875 marine and 1,625 terrestrial locations. The average number of years sampled across the time series was 9.2, with the longest time series spanning 97 years (Extended Data Fig. 2).

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

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

To test whether biodiversity responses to temperature change were modulated by the baseline climate at any given location, we extracted annual mean temperature data from the WorldClim[53] database for terrestrial time series, and from the Bio-ORACLE database[54,55] for marine time series (on a resolution of 0.01° and 0.1° for terrestrial and marine systems, respectively). For each realm, we standardized the long-term annual mean temperature across all the locations by subtracting the mean and dividing by s.d.

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

The overall model structure implemented for each realm was:

$$\Delta \text{Biodiversity} \sim 0 + \Delta \text{Temperature} \times \text{Long-term average temperature} + (0 + \Delta \text{Temperature} | \text{Taxon}) + (1 | \text{Taxon}/\text{Study ID}).$$

The meta-analytical framework implemented allows the response variables to be weighted by their uncertainty; specifically we included the estimated standard

errors for the biodiversity trends using the function se() when specifying the formula for the models, using the brms syntax[56,57]: $\Delta \text{Biodiversity} | \text{se}(\Delta \text{Biodiversity}, \text{sigma}=\text{TRUE})$. Additionally, a global intercept equal to zero was specified to reflect a scenario where there is no biodiversity change when all the independent variables are zero; that is, the model assumes that no change in temperature would correspond to no change in the assemblage metrics for the average baseline climate (that is, at the mean value across our data).

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

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

To evaluate whether uneven sampling could be driving the observed differences between the marine and terrestrial realms, we fitted models to subsets of the marine data that matched both the number of locations (1,625 time series) and the latitudinal range of the terrestrial data. We did not attempt to control for temperature change differences between realms because this is part of the signal to be modelled. We fitted the meta-analytical models to 100 random subsamples for each biodiversity metric, illustrating that the estimates for the marine realm are robust (Extended Data Fig. 5). This analysis also illustrated that a smaller sample size may have affected our ability to detect systematic biodiversity changes on land, given that confidence intervals overlapping zero occurred for several of the meta-analytical models fit to subsets of the marine data matching the number of terrestrial time series. We further evaluated that biodiversity responses did not show any clear pattern as a function of the number of years sampled, duration and start year of the time series. Although shorter time series tend to show higher rates of biodiversity change, these also tend to have higher standard errors, which are in turn accounted for within the meta-analytical framework. We further note there were no notable differences in the estimated rates of biodiversity change as a function of number of sampled years between marine and terrestrial time series. Thus, we believe the temporal heterogeneity of sampling in our data is very unlikely to drive our findings (Extended Data Figs. 6 and 7).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
All the data can be accessed through either the BioTIME database on Zenodo (https://doi.org/10.5281/zenodo.1211105) or the BioTIME website (http://biotime.st-andrews.ac.uk/).

Code availability
Code to reproduce the analysis is available on GitHub (https://github.com/lauraantao/Temp_Biodiv_Change) and in an online archive at Zenodo[59].

References
1. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
2. Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).
3. Poloczanska, E. S. et al. Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925 (2013).
4. Bates, A. E. et al. Defining and observing stages of climate-mediated range shifts in marine systems. *Glob. Environ. Change* **26**, 27–38 (2014).
5. Deutsch, C. A. et al. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672 (2008).
6. Cheung, W. W. L., Watson, R. & Pauly, D. Signature of ocean warming in global fisheries catch. *Nature* **497**, 365–368 (2013).
7. García Molinos, J. et al. Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Change* **6**, 83–88 (2016).
8. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830 (2011).
9. Dillon, M. E., Wang, G. & Huey, R. B. Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706 (2010).
10. Comte, L. & Olden, J. D. Climatic vulnerability of the world's freshwater and marine fishes. *Nat. Clim. Change* **7**, 718–722 (2017).

11. Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species of climate warming. *Science* **333**, 1024–1026 (2011).

12. Burrows, M. T. et al. The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011).

13. Darwin, C. R. *On the Origin of Species by Means of Natural Selection* (John Murray, 1859).

14. Lenoir, J. et al. Species better track the shifting isotherms in the oceans than on lands. Preprint at *bioRxiv* https://doi.org/10.1101/765776 (2019).

15. Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. & Sunday, J. M. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**, 108–111 (2019).

16. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* **2**, 686–690 (2012).

17. Sunday, J. M. et al. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* **18**, 944–953 (2015).

18. Burrows, M. T. et al. Ocean community warming responses explained by thermal affinities and temperature gradients. *Nat. Clim. Change* **9**, 959–963 (2019).

19. Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. & Levin, S. A. Marine taxa track local climate velocities. *Science* **341**, 1239–1242 (2013).

20. Suggitt, A. J. et al. Extinction risk from Climate Change is reduced by microclimatic buffering. *Nat. Clim. Change* **8**, 713–717 (2018).

21. Supp, S. & Ernest, S. Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology* **95**, 1717–1723 (2014).

22. Schipper, A. M. et al. Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Glob. Change Biol.* **22**, 3948–3959 (2016).

23. Dornelas, M. et al. BioTIME: a database of biodiversity time series for the anthropocene. *Glob. Ecol. Biogeogr.* **27**, 760–786 (2018).

24. Blowes, S. A. et al. The geography of biodiversity change in marine and terrestrial assemblages. *Science* **366**, 339–345 (2019).

25. Gotelli, N. J. & Colwell, R. K. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391 (2001).

26. Jones, P. D. et al. Hemispheric and large-scale land-surface air temperature variations: an extensive revision and an update to 2010. *J. Geophys. Res. Atmos.* **117**, D05127 (2012).

27. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. *Int. J. Climatol.* **34**, 623–642 (2014).

28. Bowler, D. E. et al. Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People Nat.* https://doi.org/10.1002/pan3.10071 (2020).

29. Brown, J., Gillooly, J., Allen, A. & Savage, V. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).

30. Edgar, G. J. et al. Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. *Sci. Adv.* **3**, e1700419 (2017).

31. Waldock, C., Dornelas, M. & Bates, A. E. Temperature-driven biodiversity change: disentangling space and time. *BioScience* **68**, 873–884 (2018).

32. Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat. Clim. Change* **5**, 695–701 (2015).

33. Pecl, G. T. et al. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**, eaai9214 (2017).

34. IPCC *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. et al.) (Cambridge Univ. Press, 2014).

35. Bates, A. E. et al. Resilience and signatures of tropicalization in protected reef fish communities. *Nat. Clim. Change* **4**, 62–67 (2014).

36. Bates, A. E., Stuart-smith, R. D., Barrett, N. S. & Edgar, G. J. Biological interactions both facilitate and resist climate-related functional change in temperate reef communities. *Proc. R. Soc. B* **284**, 20170484 (2017).

37. Devictor, V. et al. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* **2**, 121–124 (2011).

38. Bowler, D. E. et al. Cross-realm assessment of climate change impacts on species' abundance trends. *Nat. Ecol. Evol.* **1**, 0067 (2017).

39. Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* **275**, 2743–2748 (2008).

40. Menéndez, R. et al. Species richness changes lag behind climate change. *Proc. R. Soc. B* **273**, 1465–1470 (2006).

41. Bertrand, R. et al. Ecological constraints increase the climatic debt in forests. *Nat. Commun.* **7**, 12643 (2016).

42. Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. Global priorities for an effective information basis of biodiversity distributions. *Nat. Commun.* **6**, 8221 (2015).

43. Dornelas, M. et al. Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).

44. Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl Acad. Sci. USA* **104**, 5738–5742 (2007).

45. Nolan, C. et al. Past and future global transformation of terrestrial ecosystems under climate change. *Science* **361**, 920–923 (2018).

46. Ordonez, A., Williams, J. W. & Svenning, J.-C. Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nat. Clim. Change* **6**, 1104–1109 (2016).

47. Doak, D. F. & Morris, W. F. Demographic compensation and tipping points in climate-induced range shifts. *Nature* **467**, 959–962 (2010).

48. Bryndum-Buchholz, A. et al. Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Glob. Change Biol.* **25**, 459–472 (2019).

49. IPBES *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (eds Díaz, S. et al.) (IPBES Secretariat, 2019).

50. Şekercioğlu, Ç. H., Primack, R. B. & Wormworth, J. The effects of climate change on tropical birds. *Biol. Conserv.* **148**, 1–18 (2012).

51. Chao, A. & Jost, L. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547 (2012).

52. Wood, S. N. *Generalized Additive Models: An Introduction with R* (Chapman and Hall/CRC, 2017).

53. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

54. Assis, J. et al. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* **27**, 277–284 (2018).

55. Tyberghein, L. et al. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* **21**, 272–281 (2012).

56. Bürkner, P.-C. Advanced Bayesian multilevel modeling with the R package brms. *R J.* **10**, 395–411 (2018).

57. Bürkner, P.-C. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

58. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2017).

59. Antão, L. H. et al. Code relevant for the manuscript 'Temperature-related biodiversity change across temperate marine and terrestrial systems'. *Zenodo* https://doi.org/10.5281/zenodo.3708095 (2020).

60. Sunday, J. et al. Thermal tolerance patterns across latitude and elevation. *Phil. Trans. R. Soc. B* **374**, 20190036 (2019).

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Author contributions

M.D. and A.M.S. conceived the idea, and all authors contributed to the design of the project. L.H.A. analysed the data in close consultation with S.A.B., A.E.B., M.D. and A.M.S. L.H.A. wrote 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 A.E.M. all contributed to manuscript completion and revision.

Competing interests

The authors declare no competing interests.

## Additional information

a) Temperature change
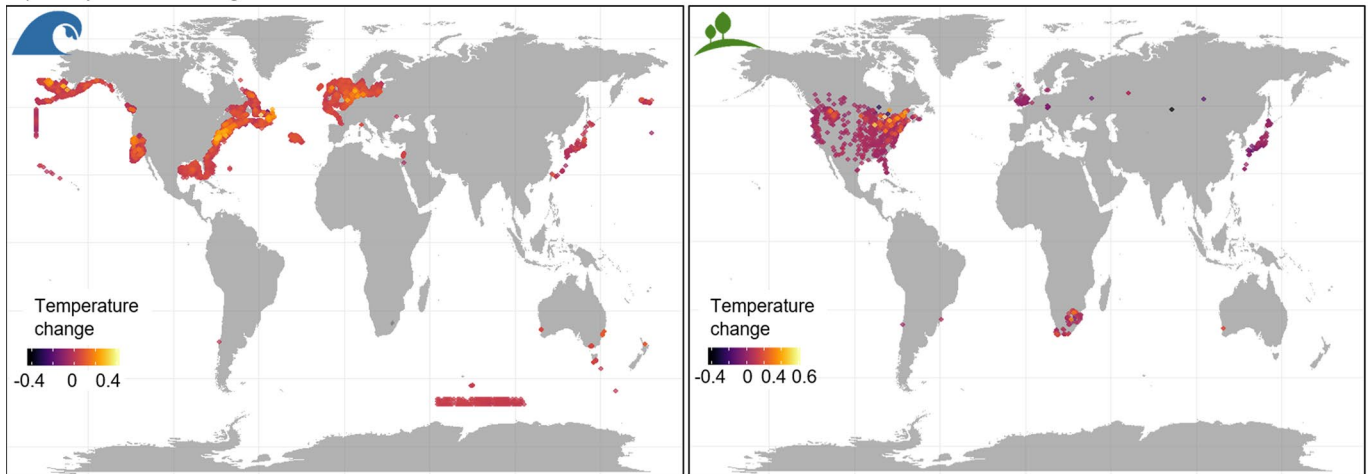

b) Species richness change
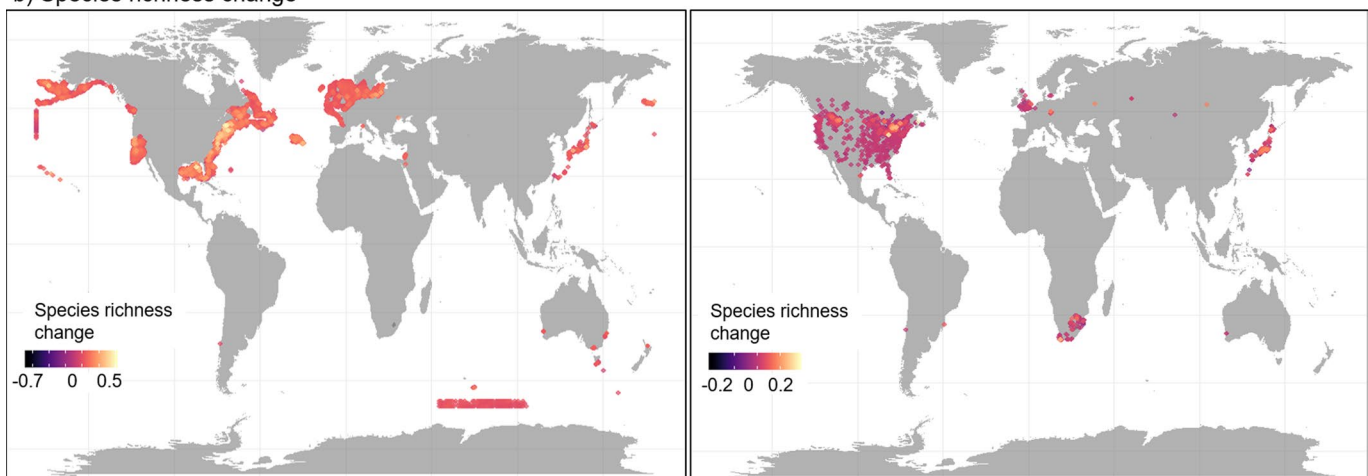
Extended Data Fig. 1 | Location of temperate biodiversity time series for each realm. Dots are coloured according to the temperature change experienced during the period of biodiversity monitoring in those locations (**a**), and with the corresponding rates of species richness change (**b**). Credit: b farias, CL (wave image) and Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/); world maps produced using the R package tidyverse v.1.2.1 (ref. [61]).

61. Wickham, H. et al. Welcome to the Tidyverse. *J. Open Source Softw.* **4**, 1686 (2019).
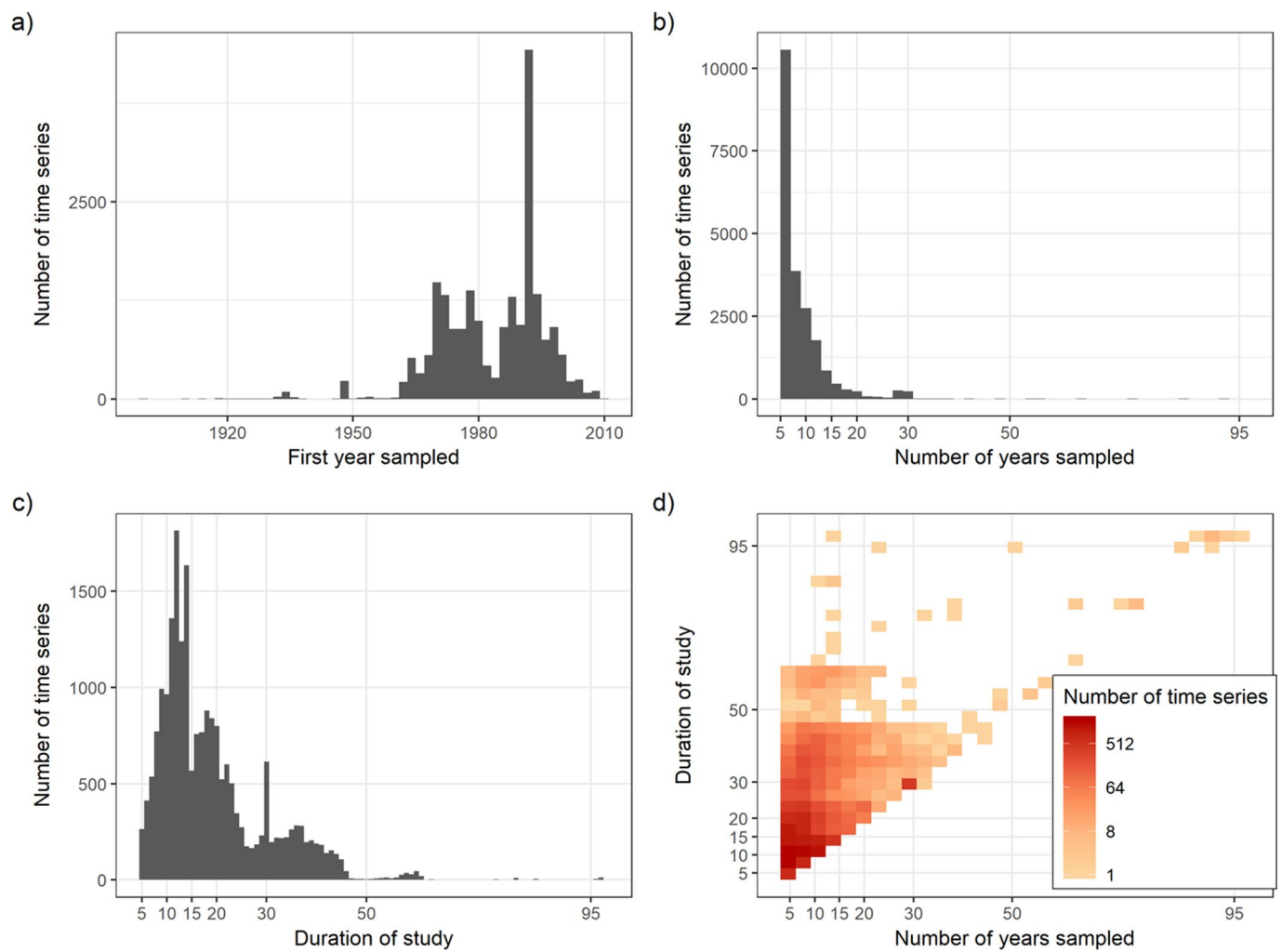
Extended Data Fig. 2 | Variation among time series regarding temporal sampling. (**a**) the starting year (binned into 2-year periods); (**b**) the number of years sampled; (**c**) the duration (time period between first and last sample) of the time series; and (**d**) duration of time series as a function of the number of samples, where colours represent the number of time series for a given combination of duration and number of samples.
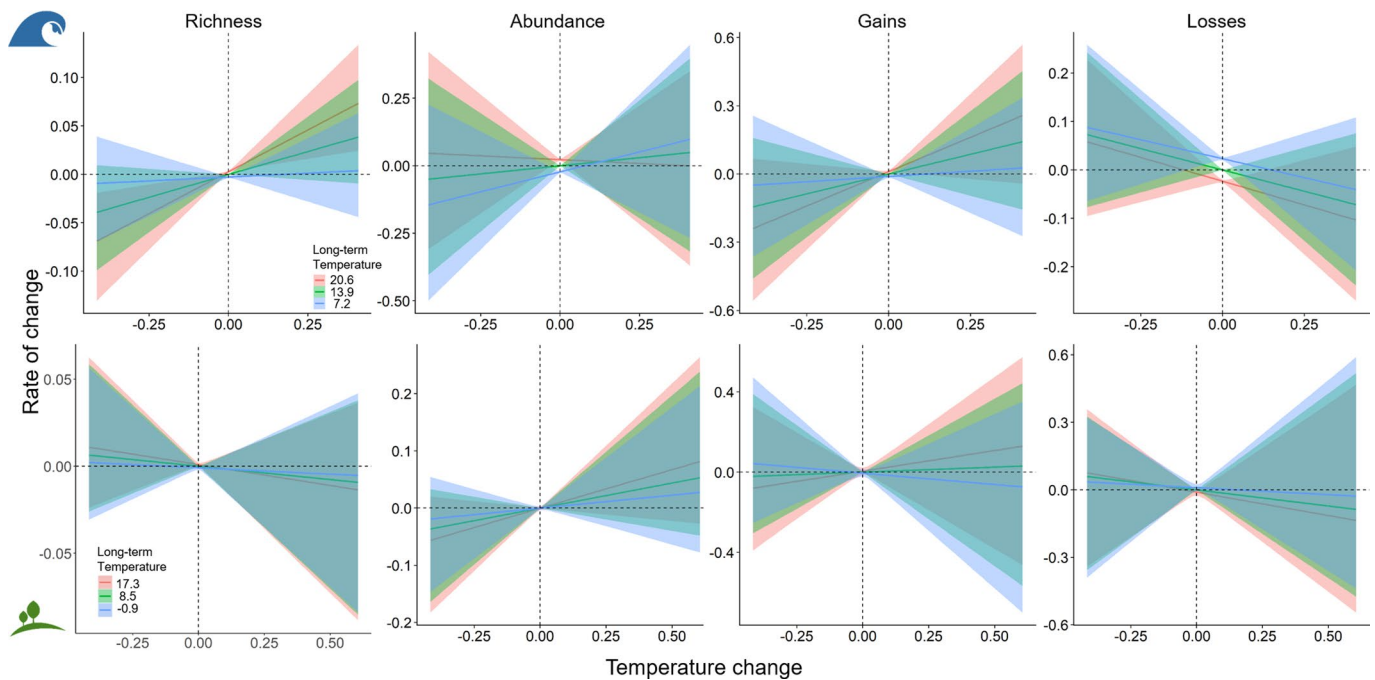
Extended Data Fig. 3 | Marginal effects of the interaction between temperature change (°C per year) and baseline climate on the biodiversity responses (rate per year). The coloured fitted lines indicate three long-term annual mean temperature values representing the range across the time series (specifically the mean ± one standard deviation for each realm), and the shaded areas represent the 95% credible interval estimated from the meta-analytical models. For each biodiversity metric, the top row is for marine locations, and the bottom row for terrestrial locations (note the different scales among metrics). Credit: b farias, CL (wave image) and Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/).
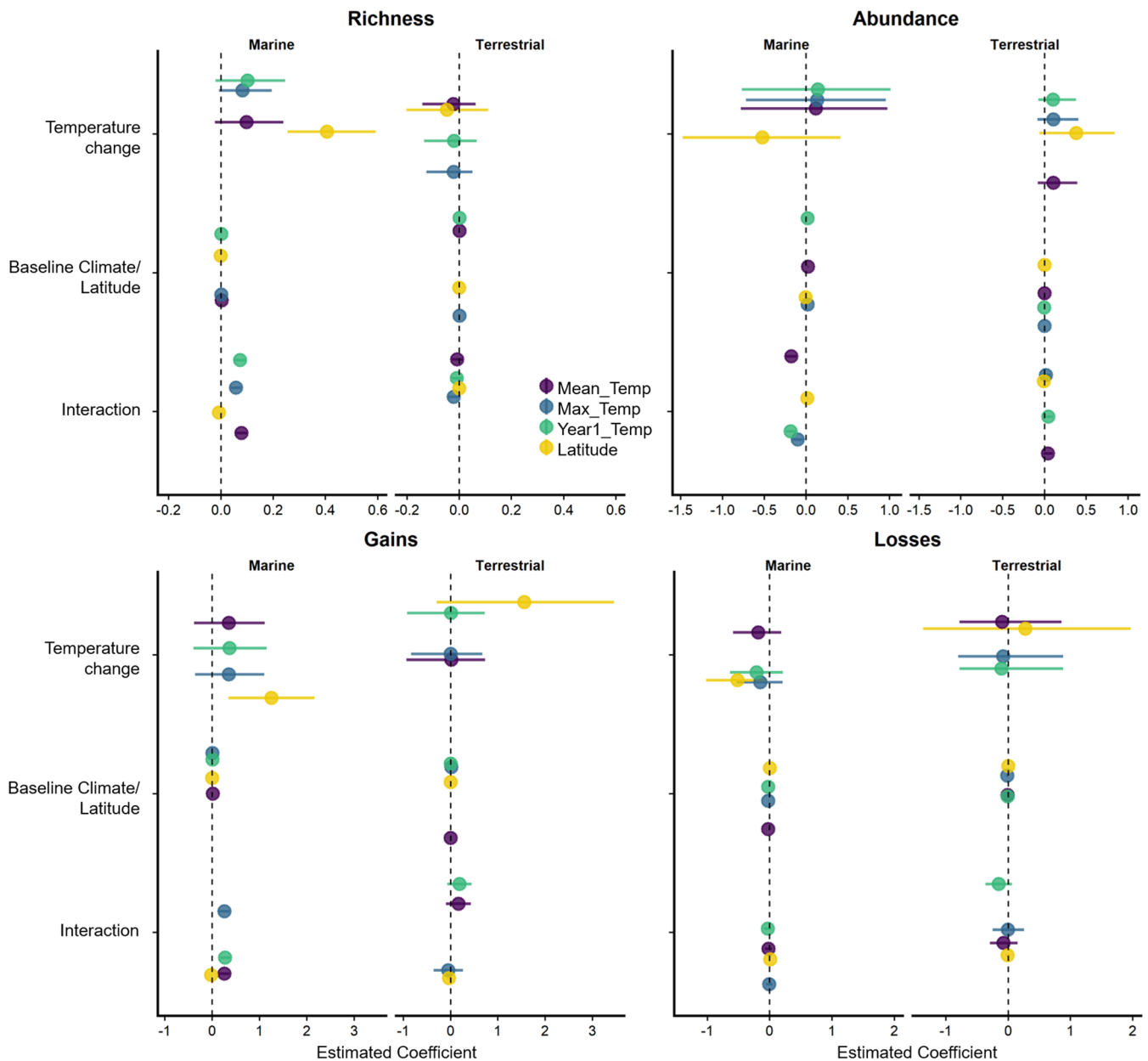
Extended Data Fig. 4 | Comparison of the meta-analytical model estimates using different variables for the baseline climate, as well as latitude. Dots represent the estimated parameters and whiskers indicate the 95% credible intervals from the Bayesian meta-analysis. Overall, our results were robust to the different temperature variables used: long-term annual mean (Mean_Temp) and maximum temperature (Max_Temp) from the databases WorldClim and Bio-ORACLE, and average air and sea surface temperature in the first year sampled from the HadCRUT4 database (Year1_Temp). Additionally, latitude did not show interacting effects with temperature change.
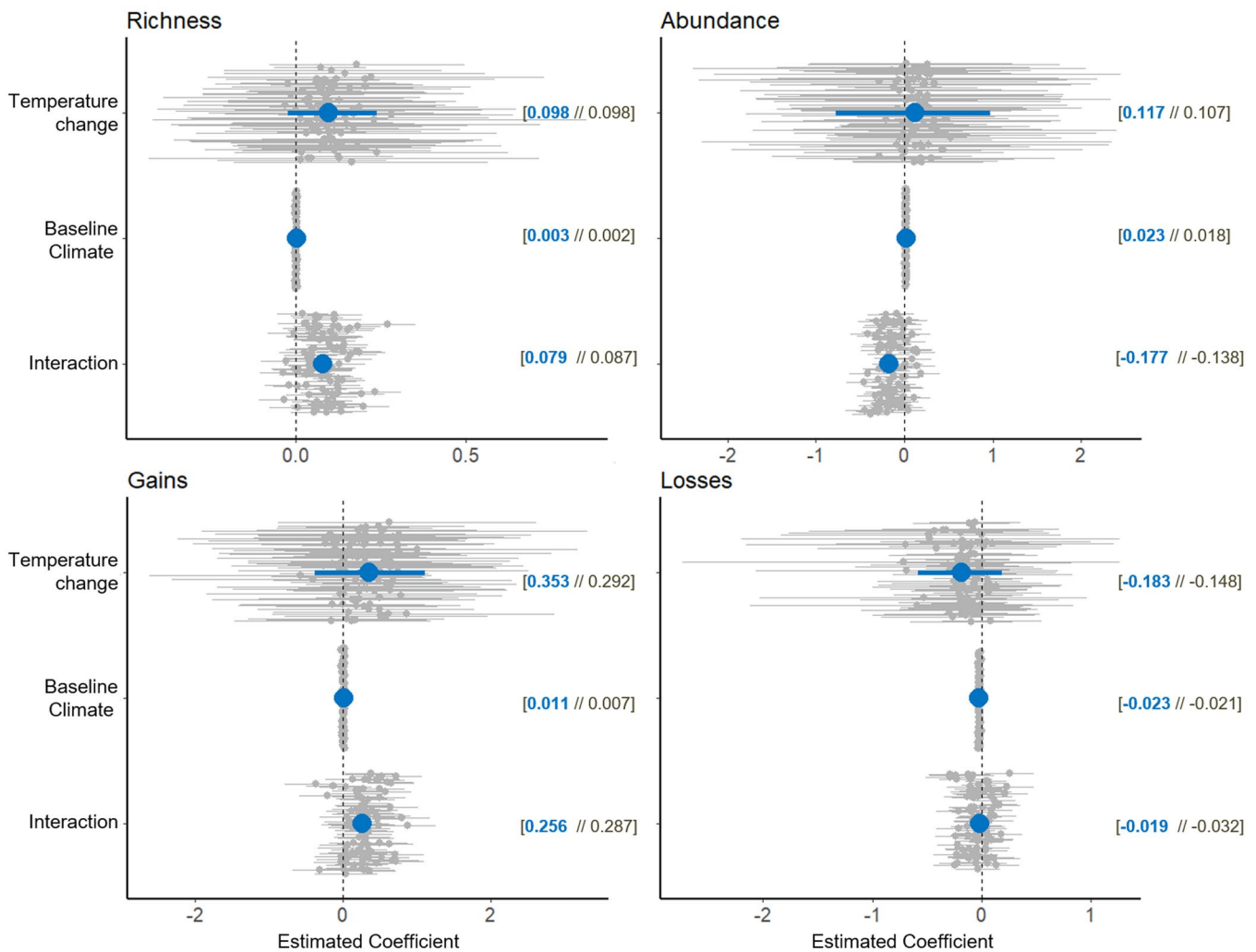
Extended Data Fig. 5 | Sensitivity analysis for each biodiversity metric. The grey points show the estimated coefficients (and their 95% credible intervals) from 100 meta-analytical models fit to subsets of the marine data, which were randomly subsampled to match the number of locations and latitudinal range of the terrestrial data. Despite the increase in uncertainty due to the smaller data subsets (that is larger credible intervals), comparing the parameter estimates based on the random sub-samples with the parameters estimated using the entire data (blue dots) shows that the marine estimates were not biased due to uneven sampling. Text insets indicate the parameter estimates for the full marine data (blue) and the average across the 100 random sub-samples (grey).
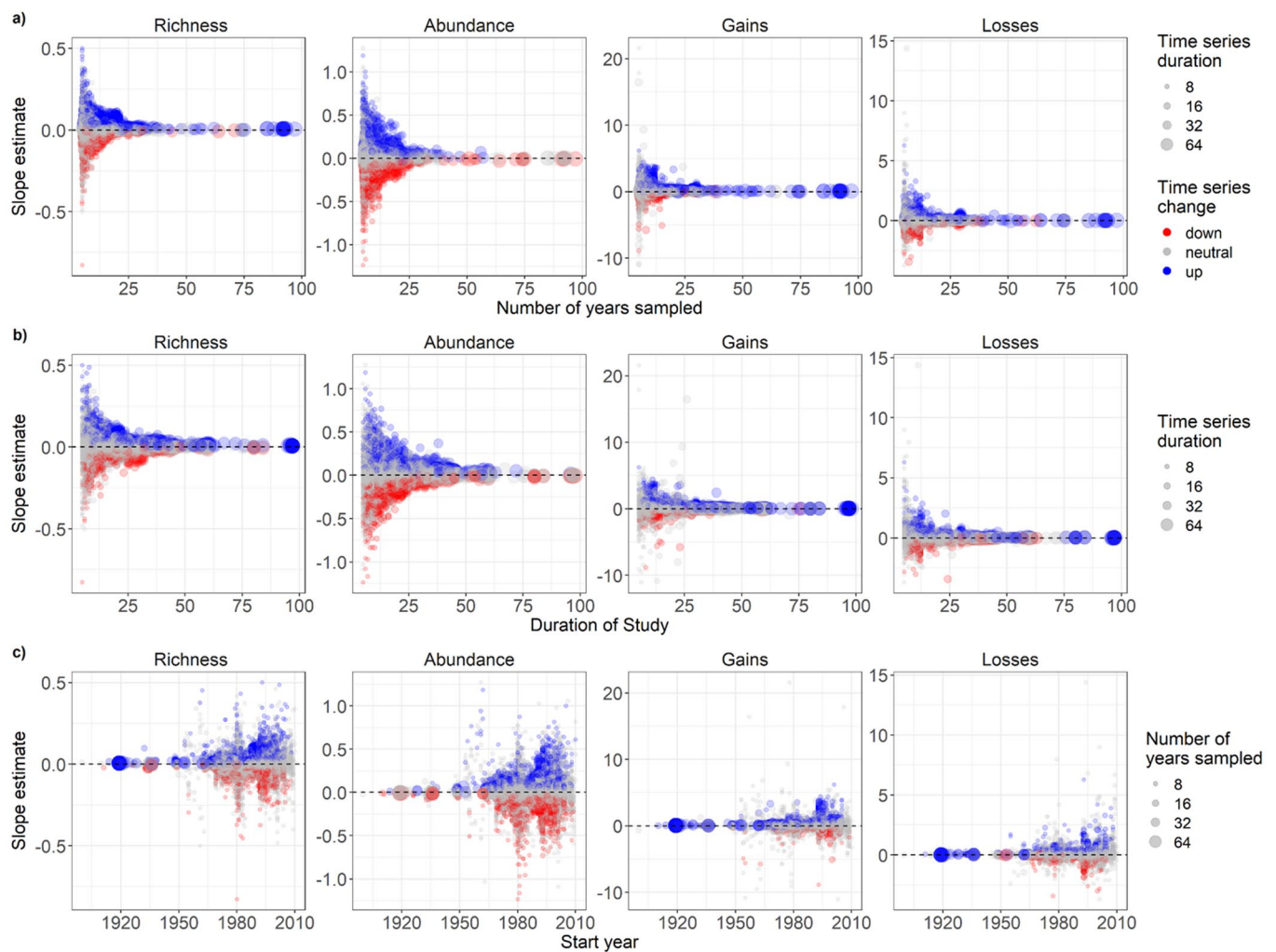
Extended Data Fig. 6 | Variation in biodiversity estimated slopes. Variation in biodiversity estimated slopes as a function of (**a**) the number of years sampled used to calculate the trends in each time series, where the size of the points represents the duration of the time series (that is Year$_{end}$ – Year$_{start}$ +1); (**b**) the duration of the time series; and (**c**) the start year of each time series, where the size of the points represents the number of years sampled. In all the plots, colours indicate whether estimated slopes were significantly positive (blue), negative (red) or neutral (that is not statistically different to zero; grey).
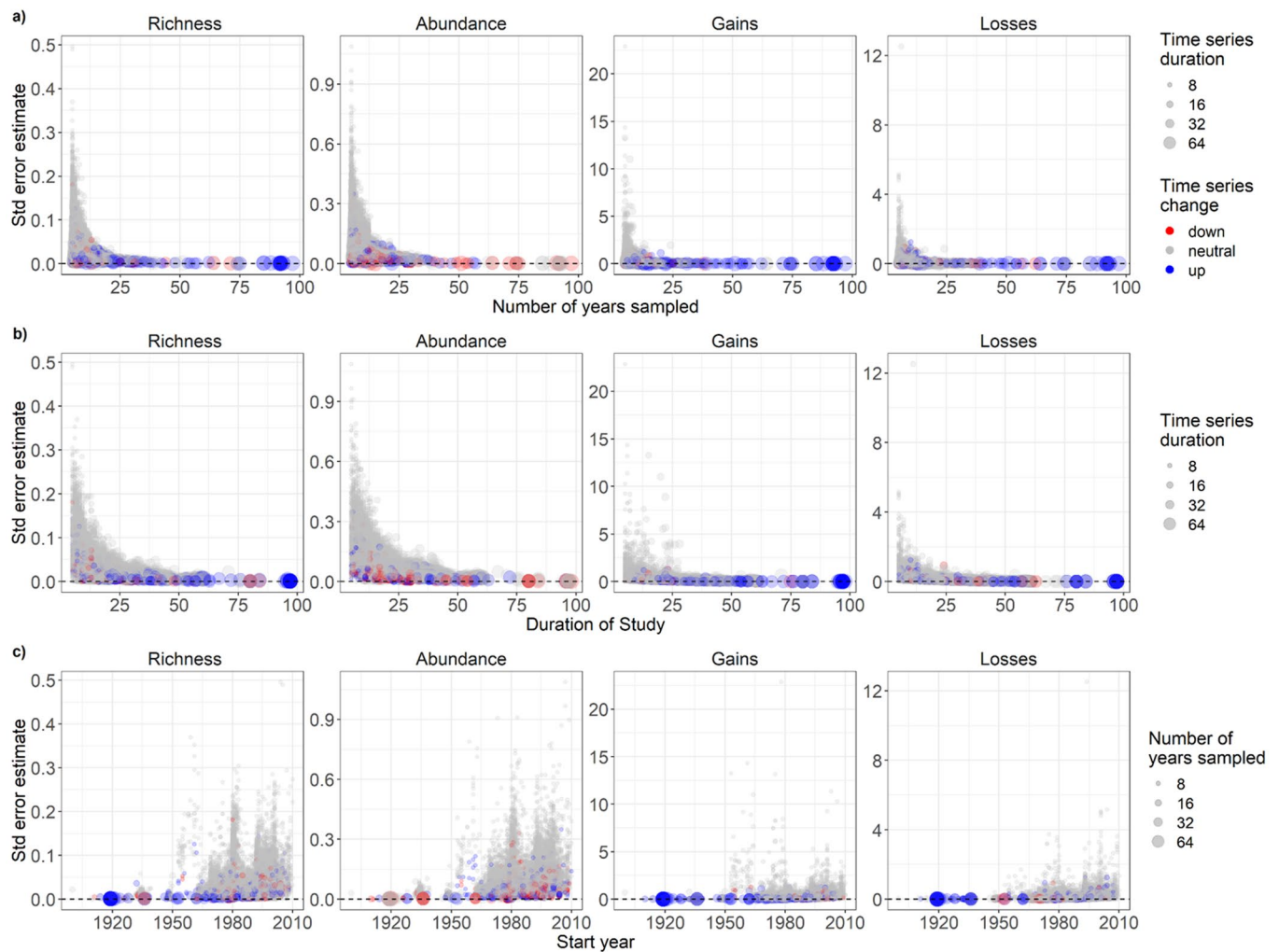
Extended Data Fig. 7 | Variation in biodiversity estimated standard errors. Variation in biodiversity estimated standard errors as a function of (**a**) the number of years sampled used to calculate the trends in each time series, where the size of the points represents the duration of the time series (that is Year$_{end}$ – Year$_{start}$ + 1); (**b**) the duration of the time series; and (**c**) the start year of each time series, where the size of the points represents the number of years sampled. In all the plots, colours indicate whether estimated slopes were significantly positive (blue), negative (red) or neutral (that is not statistically different to zero; grey).
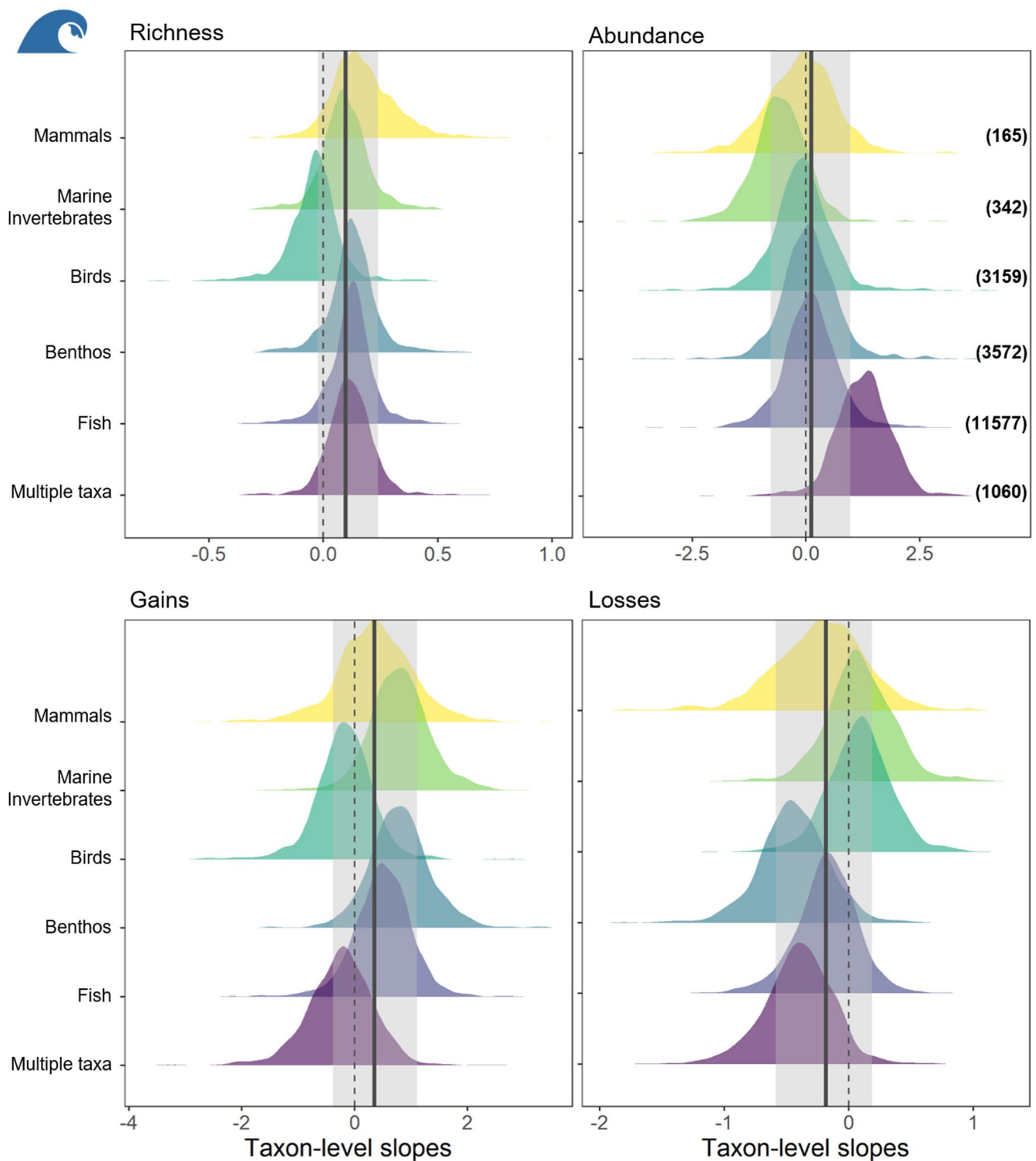
Extended Data Fig. 8 | Density plots of the posterior distributions of the estimated random slopes for the temperature change effect per taxonomic group in the marine realm. The black vertical line indicates the overall slope estimate for each biodiversity response, with the corresponding 95% credible interval as grey shading; vertical dotted lines indicate zero. The numbers in brackets indicate the number of time series for each taxonomic group (see Supplementary Tables 3–6 for complete model outputs). In two instances, these distributions showed some tendency for deviating from the overall estimated mean. Specifically, "Birds" showed more negative trends for richness change than the average across taxa, and "Multiple taxa" showed more positive trends for abundance change than the average estimate. Yet, both distributions showed extensive overlap with the other taxonomic groups, as well as with the confidence intervals for the overall mean responses. Thus, we refrain from reading too much into these patterns, given the biases in the BioTIME data, and rather focus on the general patterns of change. Credit: b farias, CL (wave image), The Noun Project (https://thenounproject.com/).
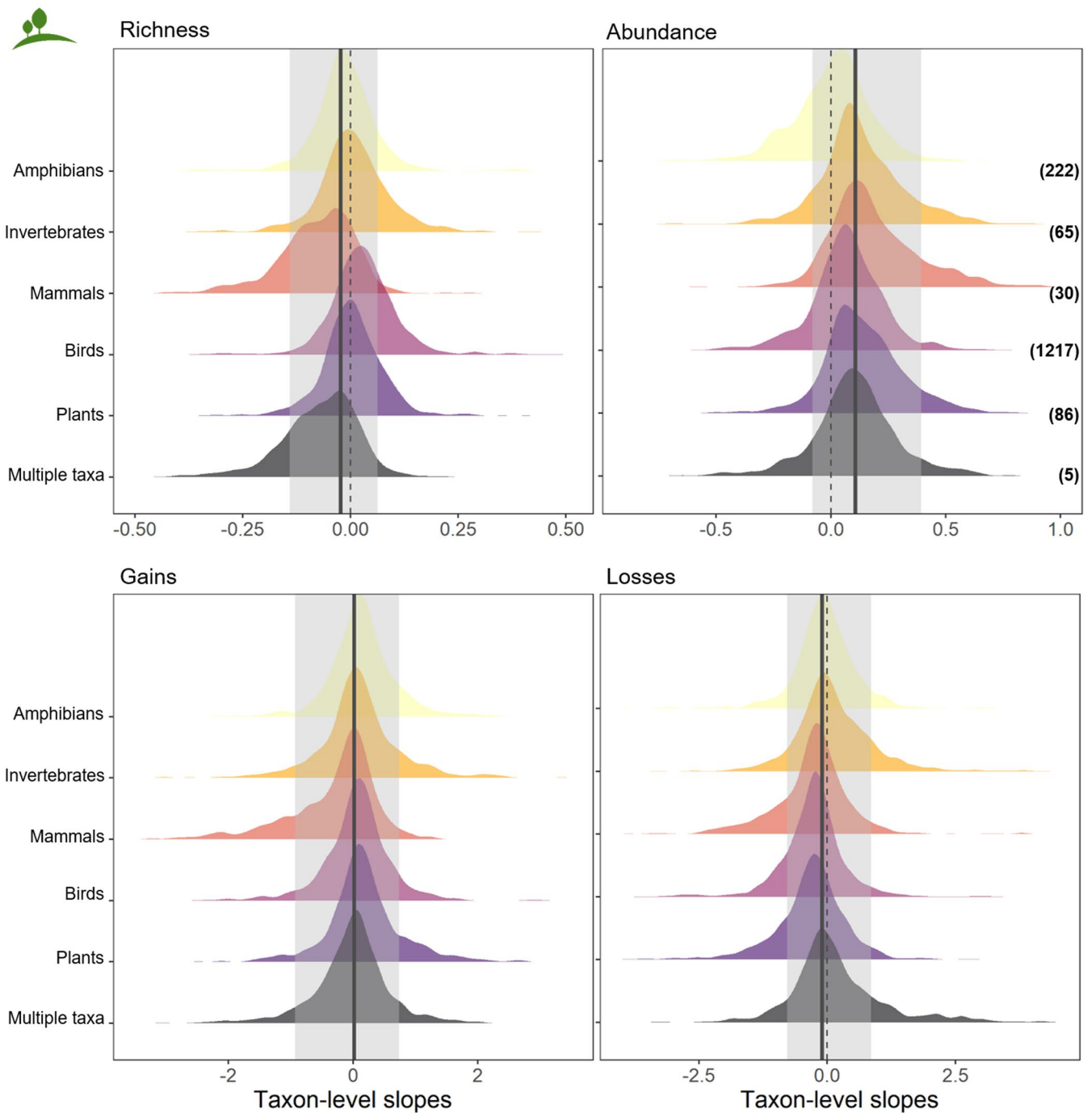
Extended Data Fig. 9 | Density plots of the posterior distributions of the estimated random slopes for the temperature change effect per taxonomic group in the terrestrial realm. The black vertical line indicates the overall slope estimate for each biodiversity response, with the corresponding 95% credible interval as grey shading; vertical dotted lines indicate zero. The numbers in brackets indicate the number of time series for each taxonomic group (see Supplementary Tables 3–6 for complete model outputs). Credit: Alexander Skowalsky, HU (tree image), The Noun Project (https://thenounproject.com/).

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Data analysis	All analyses were performed in the R software v 4.3.1; specifically we used the brms package for the modelling (version 2.6.0). Code to reproduces the analysis is available on GitHub (https://github.com/lauraantao/Temp_Biodiv_Change) and deposited in Zenodo (http://doi.org/10.5281/zenodo.3708095).

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Study description	We used data from the currently largest database of assemblage time-series, including different taxonomic groups and ecosystems. We matched the biodiversity monitoring data with local temperature records across temperate locations to test for: (1) increases in richness and abundance with warming, more pronounced in warmer regions; and (2) stronger responses to temperature change in marine assemblages compared to terrestrial ones. The total number of local time-series was 21,500 (from 156 original studies in BioTIME), with 19,875 marine and 1,625 terrestrial locations. We accounted for the uneven sampling between realms and for the effects of local climate.
Research sample	We used assemblage level time-series data available from the BioTIME database. The extensive spatial and taxonomic range of the studies included guarantees that our analysis covered multiple taxa and habitats across both the marine and terrestrial realms. The temperature data were also extracted from global freely available datasets. We matched the biodiversity and temperature records for the same time periods and at a standardized spatial resolution.
Sampling strategy	No sample strategy was applicable. We accounted for uneven sampling among years within each time-series, and between the marine and terrestrial realms in terms of number of time-series and latitudinal range.
Data collection	We selected abundance/count data from BioTIME, with at least five years of sampling.
Timing and spatial scale	The time span of the analysis was determined by the original studies. The time-series included in the analysis span between 1900 and 2016, and the average number of years sampled was 9.2. We standardized the spatial scale among studies, taxa and realms (using a gridding method). The time-series in the main analysis are located within temperate regions.
Data exclusions	From BioTIME, we excluded data other than counts of individuals, as well as time-series shorter than 5 years. For the main analysis, we further excluded data from tropical and polar locations (based on latitudinal cut-offs).
Reproducibility	The results can be reproduced by using the publicly available datasets, as well as the R code.
Randomization	For each time-series, taxonomic group and realm (marine/terrestrial) were assigned according to information from the original studies. Data was not otherwise grouped.
Blinding	The datasets included in the analysis were retrieved from multiple independent sources or publications, from across the globe, and established for different purposes. Blinding to group allocation is not relevant in our study.

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