Widespread shifts in body size within populations and assemblages

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Abstract: Biotic responses to global change include directional shifts in organismal traits. Body size, an integrative trait that determines demographic rates and ecosystem functions, is thought to be shrinking in the Anthropocene. Here, we assess the prevalence of body size change in six taxon groups across 5,025 assemblage time-series spanning 1960 to 2020. Using the Price equation to partition this change into within-species body size versus compositional changes, we detect prevailing decreases in body size through time driven primarily by fish, with more variable patterns in other taxa. Change in assemblage composition contributes more to body size changes than within-species trends, but both components show substantial variation in magnitude and direction. The biomass of assemblages remains remarkably stable as decreases in body size trade-off with increases in abundance.

One-Sentence Summary: Variable within-species and compositional shifts combine into shrinking body size, abundance increases and stable biomass through time.

Main Text:

The loss or gain of large organisms can have dramatic consequences for ecosystem functions in terms of total system biomass and metabolism, and thus food web energy fluxes (*1*). Anthropogenic changes to the biosphere are miniaturizing many communities (*1-3*) due to the selective removal of the largest individuals (population change e.g. (*4*)) and the extinction of larger species (compositional change e.g. (*5*)). Population shifts in body size have been attributed to anthropogenic selection forces, including preferential exploitation of larger individuals (*6, 7*), climate change and habitat conversion (*8-10*). At the assemblage-level, species compositional change is a major component of biodiversity change (*11, 12*). Large-bodied species have been particularly susceptible to extinction following temperature shifts (in either direction) and human exploitation, largely due to their life history traits and lower abundances (*13*). Yet shrinking trends of community body sizes are by no means universal and, when examined across many communities, some results suggest no net change in body size (*14*). Indeed, as species shift their ranges, some communities are gaining larger species, such as in arctic and high-elevation plant assemblages (*6*). Hence, the prevalence of population and compositional body size changes and their implications for assemblage abundance and biomass are unknown.

Previous assessments have investigated either compositional components of body size change (*14*) or within-species population changes (*3*), or when both components are examined, have focused on a single taxon (*15*). Yet, interactions of change in the two components can lead to non-intuitive outcomes in body size distributions through time. For example, the loss of competitors arising from compositional change can allow the remaining populations to increase in body size (*16*). Several scenarios of body size change can arise by simultaneously considering within-species population and compositional body size changes (Fig. 1). The two components can operate in the same direction (both increasing or decreasing body size), or change can involve only one component (change only in population or composition, but not both). Finally, change in one component can cancel out change in the other. Here, we explicitly set out to test to what extent each of the two components most commonly drives the changes in body size we observe across taxa and regions, and how often change in the two components occurs in opposite directions.

To examine these scenarios, we used time-series that recorded organism abundance and body size (biomass) data in the field, and quantified the contribution of both components, compositional and within-species body size changes, to change in body size distributions across taxa. Specifically, we collated 5,025 assemblages over 60 years (*17*), a time period of intensification of anthropogenic selection forces on the biosphere (*18*). These time-series range from 5-56 years of surveys and cover 4,292 species within six taxonomic groups (1971 fish sp., 1201 plants sp., 628 invertebrates sp., 66 mammals sp., 33 herpetofauna sp., and 393 marine benthic organisms) from communities distributed across multiple regions of the world (fig. S1). The time-series cover a variety of body sizes and body size change trends. We found body size shrinking in more assemblages than increasing across all datasets as well as among time-series that had stronger evidence for trends of change (lower p-values, see Fig. 2, fig. S3 and (*19*) for details).

We quantify the prevalence of different components of change (Fig. 1) by decomposing body size change of all assemblages into compositional and within-species changes by using an extension of the Price equation (*19-21*). The Price equation is a mathematical description of the relationship between statistical descriptors (mean and covariance) of selection and trait change (*22*). Although developed in an evolutionary context, this equation has direct application to the question of body size change through time if we equate competition and environmental filtering as selection ((*23*); but see also (*24*)). By examining the type of covariance in these two components of change, we can determine the relative contributions of compositional and within-species change to the observed overall change (Fig. 1B).

RESULTS AND DISCUSSION

Partitioning patterns of body size change

Our analysis shows that over all assemblages, body size is predominantly shrinking, with substantial variation in the balance of within-species change and compositional change (Fig. 3). Two thirds of the 5,025 assemblages decreased in average body size and one-third increased. In fact, both components of body size change were present in the overwhelming majority of assemblages (96.4%), with the magnitude of compositional change being greater than within-species change in 72% of assemblages. Although compositional and within-species change often occurred in the same direction (58.8% of assemblages), we found counteracting effects in 41.2% of all assemblages. For example, of the 3,415 assemblages showing within-species decreases in body size, ~35% had increases in body size associated with compositional change (within-species change < 0 and compositional change > 0, Fig. 3). This substantial variation in magnitude and direction of the two components of body size change and their interactions suggest both components need to be considered when assessing change in body size. While duration and time period of the time-series vary, our results are robust to the length of the time-series, the start and end dates, as well as intermediate states (pairwise comparisons among years; see sensitivity analysis in fig. S5-S6).

We found that trends in body size change over time vary among taxa, realm, and latitude (Fig. 4). Our confidence in estimates of body size change is highest for the most well represented taxon in our dataset–marine fish–which show a particularly evident decrease in body size (Fig. 4A). Among other taxa, the number of available time-series is lower and body size change trends are more variable. In fact, when fish are removed from our analysis, neither increases nor decreases dominate the overall body size change trends across the remaining dataset (fig. S3C). Among non-fish assemblages (e.g., benthos-mainly marine invertebrates, plants) the role of within-species and compositional changes is also more variable, but where the patterns of within-species are stronger (492 of 1116 non-fish time-series) there is a tendency towards increasing body size (57% of assemblages), counteracting the tendency observed in fish assemblages (Fig. 4A). When we compared overlapping data (assemblages and species) with an extended dataset which uses species' average body size estimates taken from trait databases (fig. S2), we found remarkable consistency for both fish and non-fish assemblages (fig. S3E-H). Nevertheless, we maintain that considering both axes of variation (compositional and within-species) is crucial to avoid potentially misleading conclusions that arise when the two components change in opposite directions. For instance, when we estimated global trends in body size change across all available datasets by fitting a Bayesian mixed-effects model, we did not detect any clear pattern of change (with or without fish; fig. S9-11) (*19*). This was true regardless of whether we use the same data as in our main analysis that directly measured body size trends, or the full extended dataset which includes 20,173 assemblage time-series with body size inferred from trait databases (fig. S2-S3) (see also (*14*)). This extended dataset also highlights that neither increases nor decreases dominate mean body size change other than in marine fish, even when there are few more (substantially more for birds) available time-series for other taxa (fig. S12). This result emphasizes that we should take caution against extrapolating or over-interpreting trait changes across taxa, particularly when data on within-species change are not available. More data are needed to determine the prevalence of body size change through time in non-fish taxa.

Despite caveats, we consistently detect the signal of shrinking body size in marine fish for both types of body size data, and regardless of whether we used ordinary least-squares (OLS) slope estimates or the Price equation approach. Our observation of shrinking among marine fish assemblages aligns with previous evidence (*25-27*). For marine fishes, these changes are often linked to the selective exploitation of large-bodied individuals by humans (*25*), to warming (*26*), and/or to decreased resource availability (*27*). Furthermore, disturbances and selective removal of larger individuals affects the age and size structure of populations, fish or otherwise, as well as the genetic structure within populations (e.g., plants (*28*)). Such responses may be particularly prevalent among fish because of the widespread effects of overexploitation. Across assemblages, it is likely that combinations of these drivers result in the high variability in trends and prevalence of counteracting effects that we observed in these time-series.

Collectively, our analyses reveal that both within-species and compositional changes combine to create high variability in the observed outcomes of assemblage-level body size changes through time. These findings highlight the importance of considering the separate and interactive effects of compositional and within-species body size change. Specifically, the community context is necessary to understand within-species change. For example, removing top predators (often the larger-body size individuals in an assemblage) can trigger mesopredator release, which alters assemblage size structure and composition (*29*). While it is possible that some of these dynamics are missed if predators and prey belong to different sampled assemblages, the assemblage level is where regulation will play out, for example, in the context of ecological carrying capacity (*30*).

The selection forces acting on body size are varied and have heterogeneous distributions in space and time. By partitioning body size change into within-species and compositional change, as we have done here, we can begin to explain the wide variation in body size change patterns through time found in literature. For example, global warming is simultaneously selecting for smaller body size (for metabolic reasons), affecting species' phenology, and causing range shifts (*2*). Global warming and species phenology effects can best be seen in within-species changes, while range shifts induce compositional change. The net result of these processes will depend on the environmental context. For example, in the Arctic Tundra, warming promotes larger shrubs (*6*), because species from warmer areas are expanding their ranges and because there are longer growing seasons. In contrast, warming is associated with smaller fish in the North Sea (*9*), although selective harvesting/exploitation is likely also contributing to this change (*31*). By considering both within-species and compositional changes in individual-level body size, alongside changes in relative abundance, future research should be able to better elucidate the mechanisms involved in how body size is changing through time.

Relationships between changes in body size, abundance, and biomass

Body size is usually tightly linked to abundance (*32*) through both metabolic (*33*) and trophic (*34, 35*) processes. This relationship can have implications for assemblage biomass mediated by a trade-off between size and abundance (*36*). Hence, we further investigated if the changes in body size were associated with changes in assemblage abundance, biomass, or both (Fig. 5; fig. S13). We found that abundance has, on average, slightly increased through time across assemblages, while the overall change in assemblage biomass is indistinguishable from zero (Fig. 5). Previously, no (*14*), or complex (*37*) relationships have been found between body size and abundance changes, although for invertebrates such a relationship is often negative (*38*). While our results confirm that the relationship between abundance change and body size change is complex and variable, there are signs that the overall reduction in body size is being counteracted by increasing overall abundance (Fig. 5A and C). Such trade-offs between abundance and body size are often expected (*32*) and affect ecosystem metabolic rate and function (*24, 39*). We detect a strong positive covariance between change in biomass and abundance (Fig. 5D), but much weaker covariance between abundance and body size, with the strongest trends among these two variables tending to negative covariance (Fig. 5C). These patterns in covariance are robust to removing fish time series from the analysis, despite the fact that overall change in body size is not detected in that case (Fig. S14). In fact, 79% of the assemblages with detectable trends in both variables have abundance increases and body size decreases. These patterns suggest that assemblage body size, abundance and biomass are linked and that change in one has implications for change in the others. There is evidence of widespread regulation of assemblage-level variables (species richness and abundance) whereby assemblages tend to return to previous levels after disturbances (*40*). The lack of a clear directional trend in biomass in our study suggests that it may be more tightly regulated than body size and abundance, which may cause trade-offs in change of the latter two variables.

Conclusions

We find evidence of widespread body size shrinking through time as a result of both population and community-level changes despite substantial variation, and overall stable assemblage-level biomass. Not all taxa contributed equally to the observed changes we report. We find the most widespread declines among fish assemblages, but a greater balance of increases and declines in other taxa. Body size is an easily measured, integrative, and important morphological trait that scales with many ecological characteristics of organisms and ecosystems, such as demographic rates, metabolism and resource requirements (*41, 42*). We reiterate pleas for more regular monitoring of body size (*43*), especially for taxa other than marine fish and ideally in conjunction with abundance estimates. Future research could focus on the implications of body size changes for ecosystem functions. For instance, cascading food web effects of shrinking body size could negatively affect human nutrition and associated economics (e.g., affecting crop plants and protein sources such as fish; (*44*). Moreover, shrinking body size through compositional change is likely to bring changes in other traits, and therefore trigger additional impacts on ecosystem functioning (*8*). Our study suggests the ubiquitous turnover in biodiversity composition currently unfolding (*11, 12*) is a profound re-shuffling of not only species, but also key characteristics of living organisms.

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Supplementary Materials

Materials and Methods

Figs. S1 to S14

Table S1

References (*46–260*)

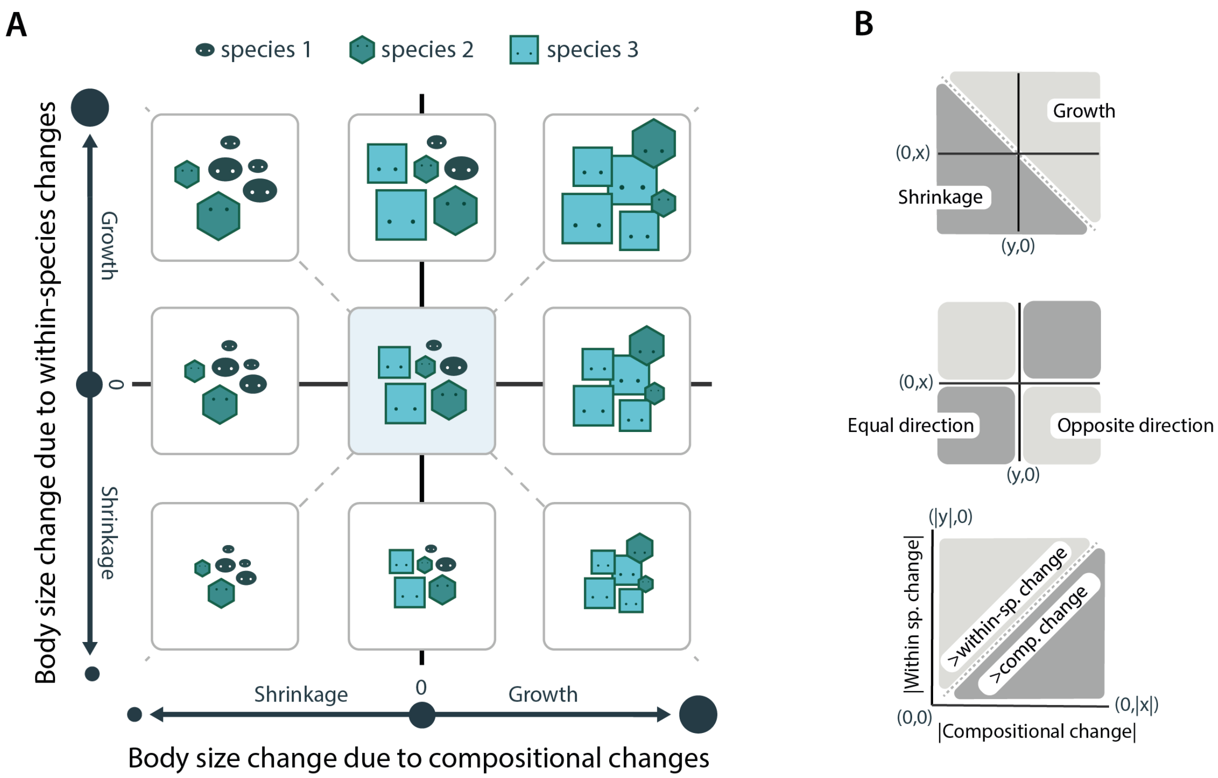

Fig. 1. Components of temporal changes in mean body size. (A) Shifts in mean assemblage-level body size can occur due to within-species changes (vertical axis), compositional changes (horizontal axis), or a combination of both components, displayed as change between two time points: from time 1 to time 2. Boxes represent assemblages made up of individual organisms (icons), with different colors and shapes representing different species. Icon size represents the body size of an individual within each species. The body size distribution at time 1 is shown in the middle (i.e., the example of no change from time 1 to time 2), with different change outcomes for time 2 shown in the other cartoons. Note that the vertical placement (axis) represents the within-species (population or intraspecific) changes through time in mean body size. This could be a mix of increases due to smaller individuals growing larger or being replaced by larger individuals (shown in the right-hand boxes) and decreases in the average size of individuals (shown in the left-hand boxes). The horizontal placement (axis) indicates change in mean body size resulting from the gain or loss of species (compositional turnover), or a change in the relative abundance of the species present in an assemblage (even without local extinction or immigration of species). **(B)** The two components of body size change can reinforce or counteract each other. Assemblage body size change is most pronounced when both components operate in the same direction (towards either shrinking or increasing body size), such that the covariance between compositional and within-species changes is positive. When only one component is involved (i.e., change in one axis but not the other), body size change tends to be lower; and with negative covariance it is possible to have change in one component cancel out change in the other (middle panel). If they counteract each other, the overall direction of change will depend on which component shows the higher absolute effect (contribution).

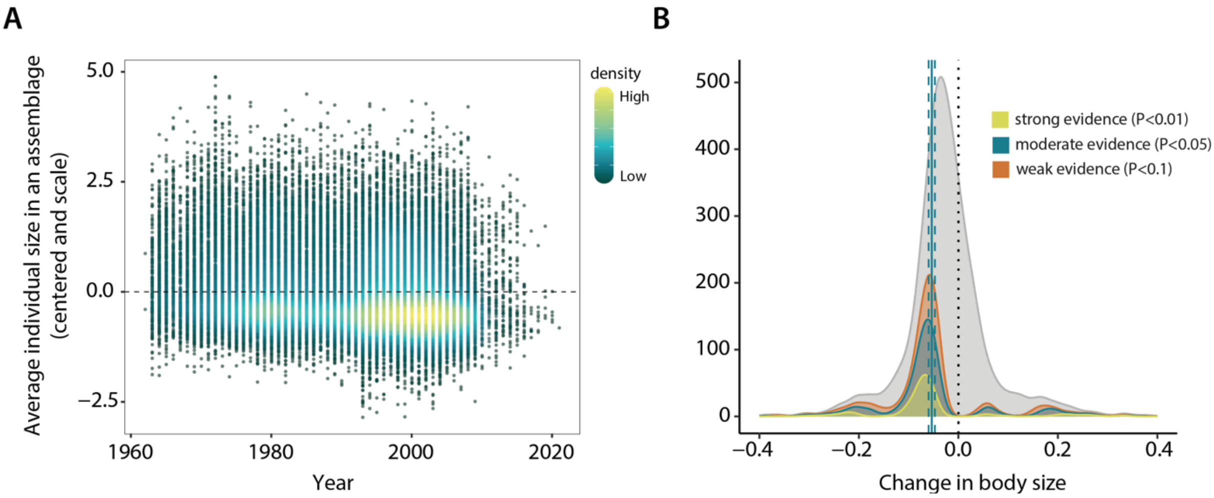

Fig. 2. Changes in mean body size across the 5,025 assemblages. (A) Average individual size across the full set of assemblage time-series. Each point is coloured by density break with colder colors indicating lower densities. **(B)** Density plots of the distribution of slopes of change in average individual body size. The full set of 5,025 assemblage time-series is shown in light gray. Yellow, blue and orange represent respectively the subset of assemblages for which strong evidence ($P<0.01$), moderate evidence ($P<0.05$) and weak evidence ($P<0.1$) of change was detected when testing slopes against 0. Dotted lines show slope of 0, while blue dashed lines show the mean slope across the blue data (traditional significance value) and the respective 90% credible interval.

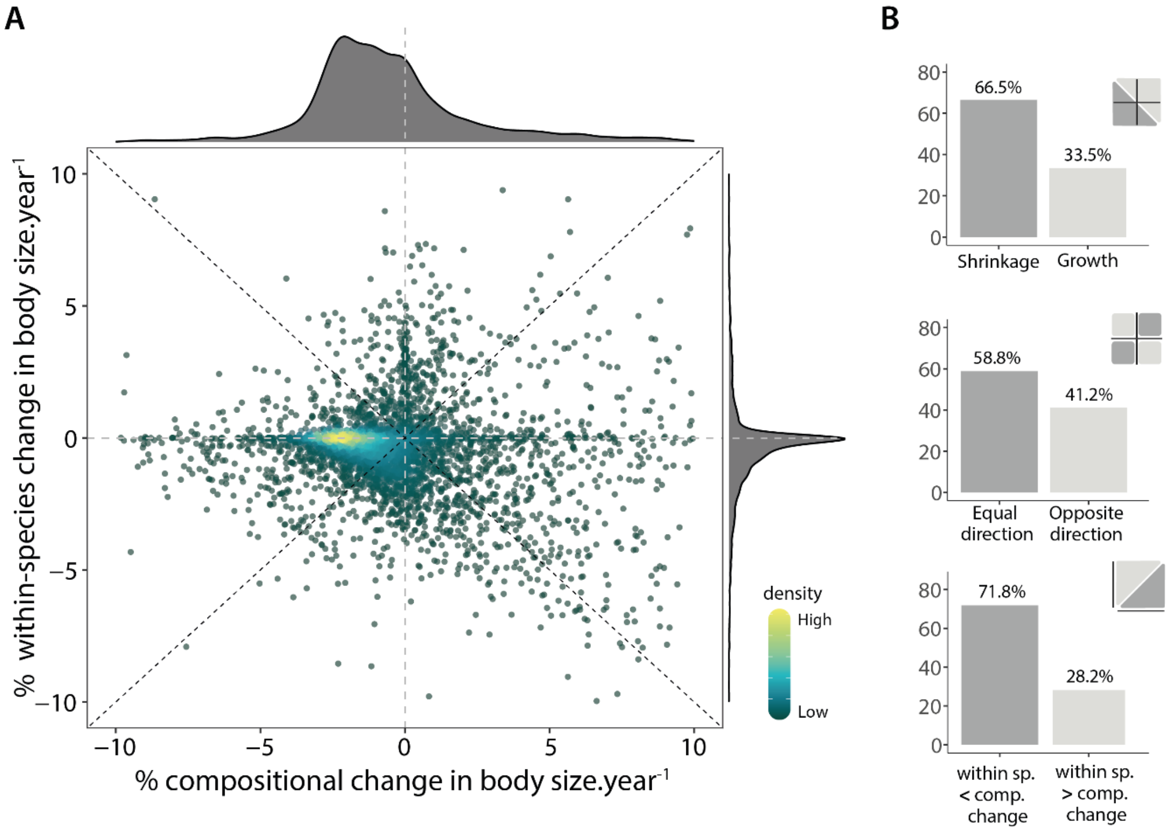

Fig. 3. Compositional versus within-species body size change through time in 5,025 assemblages representing 4,292 species of fish, plants, invertebrates, mammals, herpetofauna, and marine benthic organisms. (A) Relationship between population-level (i.e., within-species) changes and assemblage-level (i.e., compositional) changes. Both axes show % changes standardised by the number of years between the first and last year sample of the assemblage (duration); assemblages (points) are coloured by density break (colder colours indicating lower densities). Dashed lines show x = 0, y = 0, x = y and y=-x. **(B)** Frequency distributions (in percentage) of the number of assemblages (n=5025) in the different scenarios depicted in Fig. 1B. Assemblages with % change year^{-1} higher than 10% (n=517; see fig. S2 & S7) are not shown in panel (A), but are included in (B).

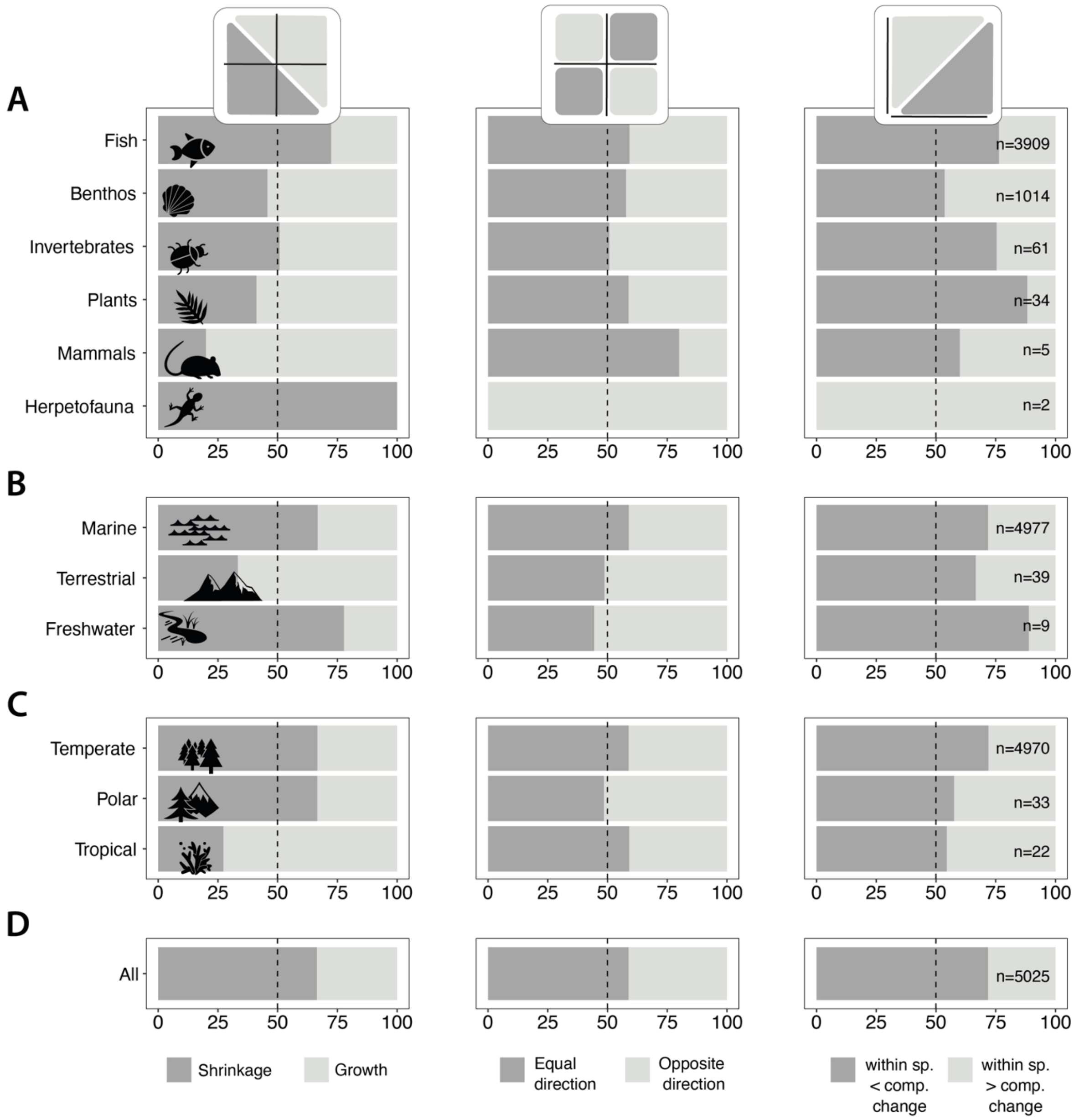

Fig. 4. Patterns of temporal body size change vary across (A) taxa, (B) realms, (C) climates, and the (D) globe. Plots show the frequency distributions (in percentage) of the number of assemblages across different groups for each scenario depicted in Fig. 1B. Dashed lines mark the 50% threshold.

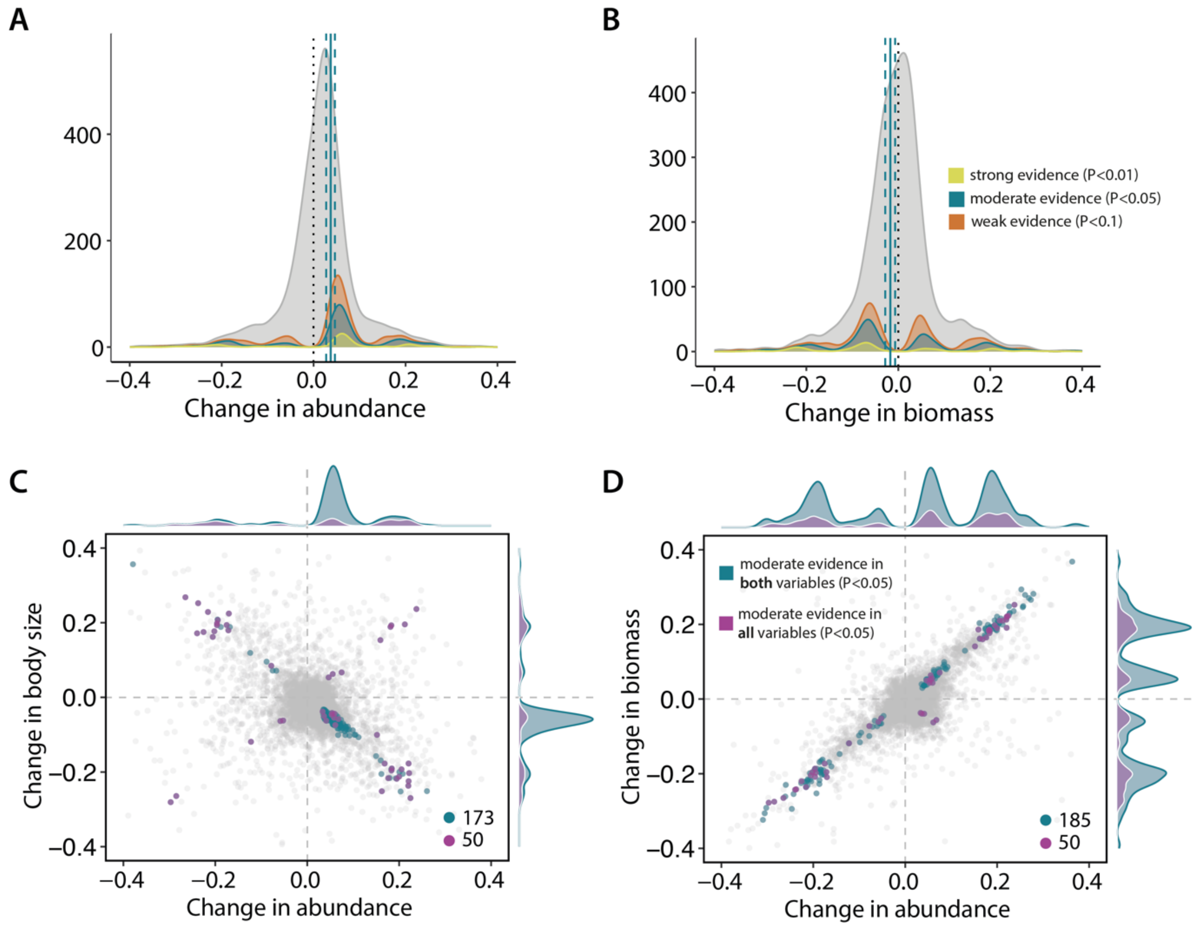

Fig. 5. Changes in assemblage abundance, biomass and body size. Density plots of the distribution of slopes of **(A)** change in total abundance of individuals (of all species), and **(B)** change in total biomass in an assemblage, as a function of time, for the same assemblages as shown in Fig. 3. The full set of 5,025 assemblage time-series is shown in light gray. Yellow, blue and orange represent respectively the subset of assemblages for which strong evidence (P<0.01), moderate evidence (P<0.05) and weak evidence (P<0.1) of change was detected when testing slopes against 0. Dotted lines show slope of 0, while blue dashed lines show the mean slope across the blue data (traditional significance value) and the respective 90% credible interval; **(C** and **D)** The bottom panels show the different relationships between variables. Only assemblages for which strong or moderate evidence (P<0.05) were detected for both variables plotted are shown in blue, while purple highlights the assemblages for which significant changes through time were detected in all 3 variables (n=50), all remaining assemblages are shown in light grey: **(C)** change in average body size as a function of abundance changes (note that 79% of the blue dots are in the quadrant where abundance increases and body size decreases), and **(D)** change in biomass as a function of abundance changes.

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Supplementary Materials for

Widespread shifts in body size within populations and assemblages.

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This PDF file includes:

Materials and Methods

Our analysis is based on bringing together trait data and ecological assemblage time-series. We used two sources of body size trait data: direct measurements of species' body size (biomass) taken over time in the field (hereafter called type 1, fig. S1) and species' average body size estimates from major published trait databases (hereafter called type 2 data, fig. S2). Both datasets of time-series cover a variety of body sizes and body size change trends (fig. S3). Below, we first describe the *a priori* quality criteria, standardisations and subsequent calculations and statistical analyses that we used to provide an analysis of the processes behind current assemblage- and population-level body size changes using type 1 data. The results of these analyses are presented in the main text. Then, we present the methodology we followed to explore the global patterns of body size change when considering compositional changes alone and using different types of trait data (type 1 and type 2; see *Supplementary Analysis* section).

<u>Assemblage time-series data (BioTIME Database)</u>

BioTIME is the largest global, open-access database of assemblage composition time-series (*17*). This database includes data on multiple multicellular taxa (e.g., plants, fish, birds, mammals, invertebrates), with over 12.5 million species-level records representing ~46,000 species. Each BioTIME study contains distinct samples measured (with a consistent methodology) over time, which could be fixed plots (i.e., 'single-site' studies where measures are taken from a set of specific georeferenced sites at any given time) or wide-ranging surveys, transects, tows, and so on (i.e., 'multi-site' studies where measures are taken from multiple sites that may or may not align from year to year). Because the spatial extent varies across studies, we followed previous approaches (*11, 46*) to identify and standardise 'multi-site' studies using a global grid of 96km^2 hexagonal cells using dggridR (*47*). Studies that were contained within a single cell were not partitioned. Following this step, each sample was assigned a different combination of study ID and grid cell (based on its latitude and longitude) resulting in a unique identifier for each assemblage time-series within grid cells, thus allowing for the integrity of each study and each sample to be maintained. Then sample-based rarefaction was applied to standardise the number of samples per year within each time-series (*11, 46, 48*). Finally, we only retained observations sampled after the year 1960 (99.4% of all the data was recorded after this period) and restricted our analysis to time-series with at least five different sampled years. For the analyses presented in the main text, we further subsetted the database, and considered only records that contain both abundance information (i.e., counts of the number of individuals) and biomass estimates directly measured in the field. In total, we considered 5,025 time-series from 45 studies across the globe (fig. S1; Table S1).

<u>Trait data (BioTIME Database)</u>

We extracted body size trait data directly from BioTIME using both abundance and biomass estimates measured at the same time and place. From each record i, we estimate average body size of individuals (BS) by considering that:

$$BS_{r,s,t,i} = \frac{B_{r,s,t,i}}{N_{r,s,t,i}},$$

where B is biomass and N is abundance recorded in year t, for species s within the assemblage time-series r. Note that biomass is only measured at the individual scale (abundance=1) for ~22% of the data, thus we refer to this measure as average individual body size. Here, we include all taxonomic groups for which the appropriate data were available including groups poorly represented in most trait compilations (e.g., invertebrates). In total, we considered the following taxon groups: fish, benthos, plants, mammals, invertebrates, and herpetofauna (reptiles and amphibians). We did not distinguish taxa across realms, but studies that included multiple taxa (i.e., studies that sampled multiple taxon groups simultaneously) were re-classified based on the dominant taxa represented. On average, we estimated multiple body size measurements for 4,292 species within the 5,025 assemblage time-series (average ~39 species per assemblage time-series; fig. S1).

Partitioning body size change – Price equation

To partition temporal changes in average individual body size, we used an extension of the Price equation (*20, 22*), that allows an exact partition of trait change, Δz, in an observed dataset:

$$\Delta z = \Sigma(\Delta q_s) z_s \ + \Sigma \ q'_s(\Delta z_s)$$

The first term on the left-hand side of the equation for Δz accounts for total body size change caused by changes in frequency due to species selection, i.e., changes in the relative abundance or presence of species with a certain property value (body size; e.g., local extirpations or colonisations). This term reflects the effect of species turnover. The second term describes the part of total change caused by changes in mean property values, reflecting the effect of within-species variation (e.g., larger individuals within a species being replaced by smaller individuals of the same species). Together, the two terms sum up to the actual change in community-weighted mean (CWM) body size in an assemblage, Δz. Given this, we quantified changes in frequency as Δq_s=q'_s- q_s, where $q_s$and q'_s are, respectively, the before and after relative abundance of species *s*; and changes in mean property value as Δz_s= z'_s- z_s, where z_s and z'_srepresent, respectively, the before and after mean individual body size of species s. In assemblage time-series where multiple individual $BS_{r,s,t,i}$ estimates were available for the same year and species (e.g. when the assemblage was monitored more than once a year), an abundance-weighted mean was used instead. Finally, when z_s was not available (i.e., colonisations did not occur) we considered z_s = z'_s for that species, and thus $\Delta z_s$is equal to 0 and no change occurs due to changes in mean property values (within-species changes).

For each assemblage time-series, we used the Price equation to partition body size changes that occurred between two years, the last year (t_2) and the first year (t_1), where $t = t_2 - \ t_1 + 1$ is the full length of the assemblage time-series. In order to ensure comparability among time-series of different durations, both the within-species and the composition component of body size change were converted to proportional changes relative to the starting size of the assemblage. This was done by dividing each component of change by the initial assemblage CWM and standardising it by duration (i.e., dividing by t). These quantities were expressed in units of % change.year^{-1}. Patterns across all assemblages are represented in Fig. 3 and fig. S4, and patterns across the different taxa, realms and climates are shown in Fig. 4.

Sensitivity analyses

Many of the assemblage time-series varied in length (27.3 ± 12yr, mean ± SD), with varying start and end points. To examine whether our results were sensitive to such effects, we repeated the analysis using alternative start (t_1) and end times (t_2) within the same assemblage. This analysis included a scenario where the first year was fixed, a scenario where the last year was fixed and a scenario where both years varied randomly. For each of the three scenarios, we repeated the analysis 100 times, where for each iteration we used the Price equation to partition body size changes that occurred between the selected two years in a given assemblage (as done in our main analysis); and reported the median effect of each component and their dispersion (interquartile range) across all iterations (fig. S5). Additionally, we also used the Price equation to partition body size changes that occurred between all pairs of consecutive years in a given assemblage, to investigate the bias found in intermediate states (fig. S6). Despite slight differences across scenarios, the results were largely concordant and yielded the same directional trends.

Given that some of the estimates were extreme with very large changes to assemblage level body size (~0.7% of assemblages show increases in compositional change in body size.year^{-1} >100%; fig. S4), there could be some concerns about errors in the measurement or measurement reporting of the abundance and biomass estimates (and consequently body size estimates) in the original datasets. We performed in-depth checks of the raw data within affected individual datasets (see fig. S7 for an example) and found that such effects seem to be a true representation of changes occurring in the assemblages. Nevertheless, these few assemblages have the potential to over-influence the overall effects found, so we chose to report robust statistics (median and interquartile range) that de-emphasise such extreme cases without removing them, when appropriate (e.g., fig. S5 and S8).

For some assemblage time-series the sample-based rarefaction process could lead to a different species composition. To ensure our results were robust to the random samples selected by the sample-based rarefaction process, we performed a bootstrap analysis re-running the analysis described in the main text (using first and last year only) 100 times, each time using a different dataset after the sample-based rarefaction process was applied. Only the results of one iteration are presented in the main text, but plots of the distribution of results across the 100 rarefaction iterations can be seen in fig. S8.

Supplementary Analyses

At large scales and often using species-level trait values, previous studies generally conclude that body size has, on average, been decreasing (*2, 3, 27*). This is due both to compositional changes, whereby bigger species are disproportionately replaced by smaller species (*3*) and within-species changes associated with the removal of larger individuals (*42*). However, data limitations on individual-level body size make it difficult to assess the importance (and signal) of the latter, thus, constraining global assessments to quantify body size change using species-level trait values alone. Here, we follow a similar approach but use BioTIME data to test if the assemblage body size shrinkage patterns presented in the main text are observed at the global scale when using different types of trait data. For this analysis, we used two distinct subsets of BioTIME data: the 45 studies with directly measured estimates of body size (as described earlier in the Materials and Methods; type 1 data), and a larger subset of studies for which estimates of body size could be retrieved from major published databases (species trait averages; type 2 data). Note that when matching with trait databases (i.e., the type 2 data), we did not work with only the subset of 45 studies featured in the main text but considered instead all BioTIME data that reported counts of the number of individuals and met our duration criteria. The different steps of data preparation and analysis for the former (type 1) are summarized earlier in the Materials and Methods of this document (*19*), any additional data, statistical analyses and supplementary results are described in detail below.

Additional Trait data (Trait databases)

Five open-access global databases were identified as having partially overlapping observations with species listed in the BioTime dataset: AmphiBIO (*49*); https://doi.org/10.6084/m9.figshare.4644424.v5), TRY database (*50*); https://www.try-db.org/), EltonTraits 1.0 (*51*); https://doi.org/10.6084/m9.figshare.c.3306933.v1), FishBase (*52*); www.fishbase.org) and Carabids.org (*53*); http://www.carabids.org). While a number of traits related to body size are available in these datasets, here, and given the broad-scale goal of the paper, we choose to select the body size trait that had the higher cover for each taxon. For birds and mammals, it was body mass ('*body_size_mm'* field). However, for ectotherms, length was used instead, as it is a more commonly available measure and considered more reliable than body mass. For fish and beetles (hereafter: Invertebrates) we used maximum body length (*'MaxLengthTL'* and *'maxSize'* fields, respectively), for amphibians we used snout-vent length (*'body_size_mm'* field), and for plants we used plant height (*'veg_height'* field). Only species-level trait values were considered and when there were multiple values for a particular species (i.e., TRY database), we took the median.

Synthesis and harmonisation of data

To merge and harmonise the assemblage time-series and trait databases data and optimise species matching, we first followed a series of steps to deal with species names and incompatibilities between the two sources of data. As a preliminary step, we reviewed species names listed in BioTIME with the taxize R package (*54*). An additional field was created with potential synonyms, or alternative scientific names (identified misspelling errors). Finally, common names were also flagged and, when possible, converted to scientific synonyms using additional data sources (ITIS and NCBI), helped by manual inspection based on the description provided. This process allowed for 913 species (11%) extra matches between the two sources of data. Because the sample-based rarefaction could result in different species composition for some assemblage time-series, we decided to work with all 100 BioTIME resamples (see '*Sensitivity analysis*' section in Material and Methods (*19*)). The matching was then done for each BioTIME resample dataset separately, and filtered to keep only records from where trait values were available (i.e., common species across datasets). On average, we retained records for ~5,000 species across ~20,200 assemblage time-series (fig. S2), with an average of ~75% completeness (i.e., proportion of species in the assemblage time-series from which trait data was retrieved).

Calculating body size

The way we calculated average body size of individuals in a given year ($\widehat{BS}_{r,t}$) depended on the source of the trait data. For assemblages time-series matched with trait databases data (type 2 data), $\widehat{BS}_{r,t}$ was calculated, by averaging all species' individual body sizes, weighted by their abundances within the assemblage. For assemblage time-series with directly measured estimates of body size (type 1 data), we first calculated for each year assemblage-level total abundance and total biomass by tallying the number of individuals and biomass (regardless of species) sampled within that year, respectively. The average individual size in a given year ($\widehat{BS}_{r,t}$) was then retrieved by dividing the sum of the biomass by the total abundance reported in that year for that assemblage time-series. To make all body size estimates comparable, all values were standardised using classic z-scores, where individual observations in a group are scaled relative to the mean and standard deviation of all observations of that group. This was done for each assemblage time-series within each dataset separately.

Statistical analyses - Models of body size change

We explored the global patterns of body size change using mixed-effects models. Year (mean-centered) was included as a fixed effect, and was also included as a random slope varying across studies and assemblages, with assemblages nested into the original studies from which they originated in order to account for the non-independence of the time-series. All statistical models were fitted in a Bayesian framework using the package ‘brms’ (*55*) in R (v3.6.3; (*56*)). We modelled average individual body size change assuming a skew-normal distribution and an identity link function. The overall model structure implemented using the bms syntax was:

$$y_{j,i,t} \sim SkewNormal(\mu_{j,i,t}, \sigma, a),$$

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

where $y_{j,i,t}$ is the average individual body size change in year t of the ith assemblage in the jth study. $year_{j,i,t}$ is the time in years, β_0 and β_1 are the global intercept and slope (fixed effects), β_{0j} and β_{1j} are the study-level departures from β_0 and β_1 (respectively; study-level random intercept and slope), and $\beta_{0j,i}$ and $\beta_{1j,i}$ are the (nested) assemblage-level departures from $\beta_{0j,i}$ and $\beta_{1j,i}$ (respectively; assemblage-level random intercept and slope). We used weakly regularizing priors for the global intercept and slope, residual variation (σ), and skew parameter (a):

$$\beta_0 \sim N(0,2),$$

$$\beta_1 \sim N(0,1),$$

$$\sigma \sim student\ t(3, 0, 2.5),$$

$$a \sim N(0, 4).$$

Group level parameters were drawn from the student-t distribution:

$$\sigma_{0j} = \sigma_{1j} = \sigma_{0ji} = \sigma_{1ji} \sim student\ t(3, 0, 2.5).$$

Correlations between levels of the grouping-factors were estimated using the Cholesky decomposition (L) of the correlation matrix, with a Lewandowski-Dorota- Joe (LKJ) prior:

$$L \sim LKJ(2).$$

The model was fit to 100 resamples of each dataset (i.e., type 1 and type 2) to adjust for any variation in species composition arising when sample effort was standardised using sample-based rarefaction. For each model fit, we extracted the 100 draws from the posterior distribution, which were combined for making inferences.

Body size, abundance, and biomass change

As mean body size emerges from the ratio of biomass and abundance (see section *"Trait data (BioTIME Database)"*), change in either biomass or abundance can be responsible for any observed body size changes. To explore these effects, we quantified trends in biomass and abundance across individual assemblage time-series with directly measured estimates (type 1 data). This was achieved by fitting ordinary least-squares (OLS) regression models for each assemblage separately, with either average individual body size, total abundance, or total biomass (centered and scaled) as a function of time (year, mean-centered). All sampled years were considered. The set of slopes (β) of these linear models is shown in Fig. 2 (change in body size) and Fig.5A and B (change in abundance and biomass, respectively). Additionally, we evaluated the associations between the temporal trends in total abundance, total biomass, and mean body size, by comparing the slopes of change of assemblages for which statistically significant trends were found across two or more variables (Fig. 5C and D; fig. S13-14). Lastly, the same approach was used to explore the variability of body size change trends present in type 1 and type 2 data (fig. S3). All calculations and statistical analyses were performed in R-3.6.3 (*56*).

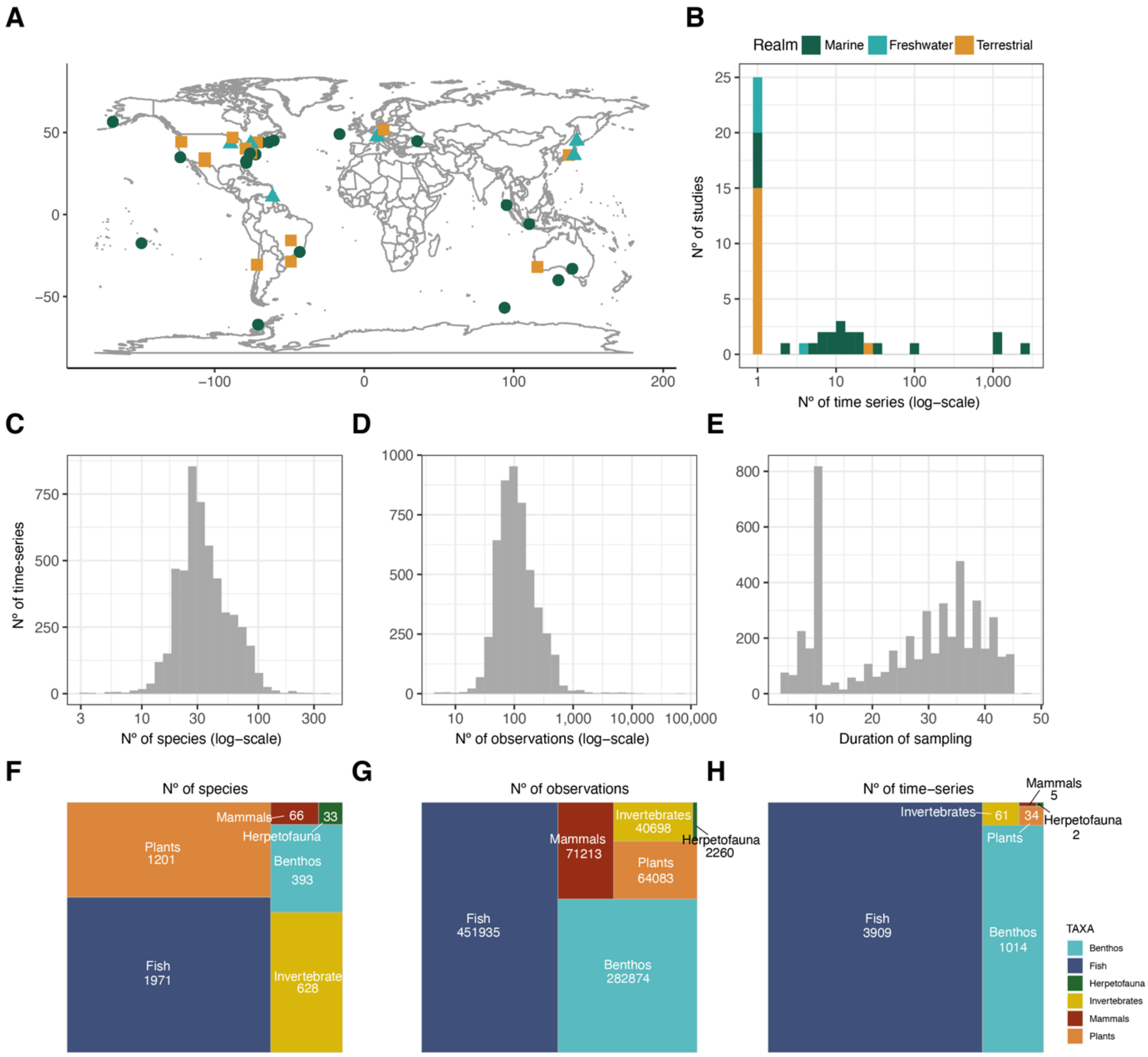

Fig.S1.

Distribution of study data characteristics (BioTIME data, type 1). (A) Location of the studies with direct measures of body size (based on central coordinates; n=45), **(B)** number of assemblage time-series in each study, **(C)** species richness observed across assemblages, **(D)** total number of body size observations across assemblages, **(E)** duration of sampling, and taxonomic distribution of: **(F)** species represented, **(G)** body size observations and **(H)** assemblage time-series.

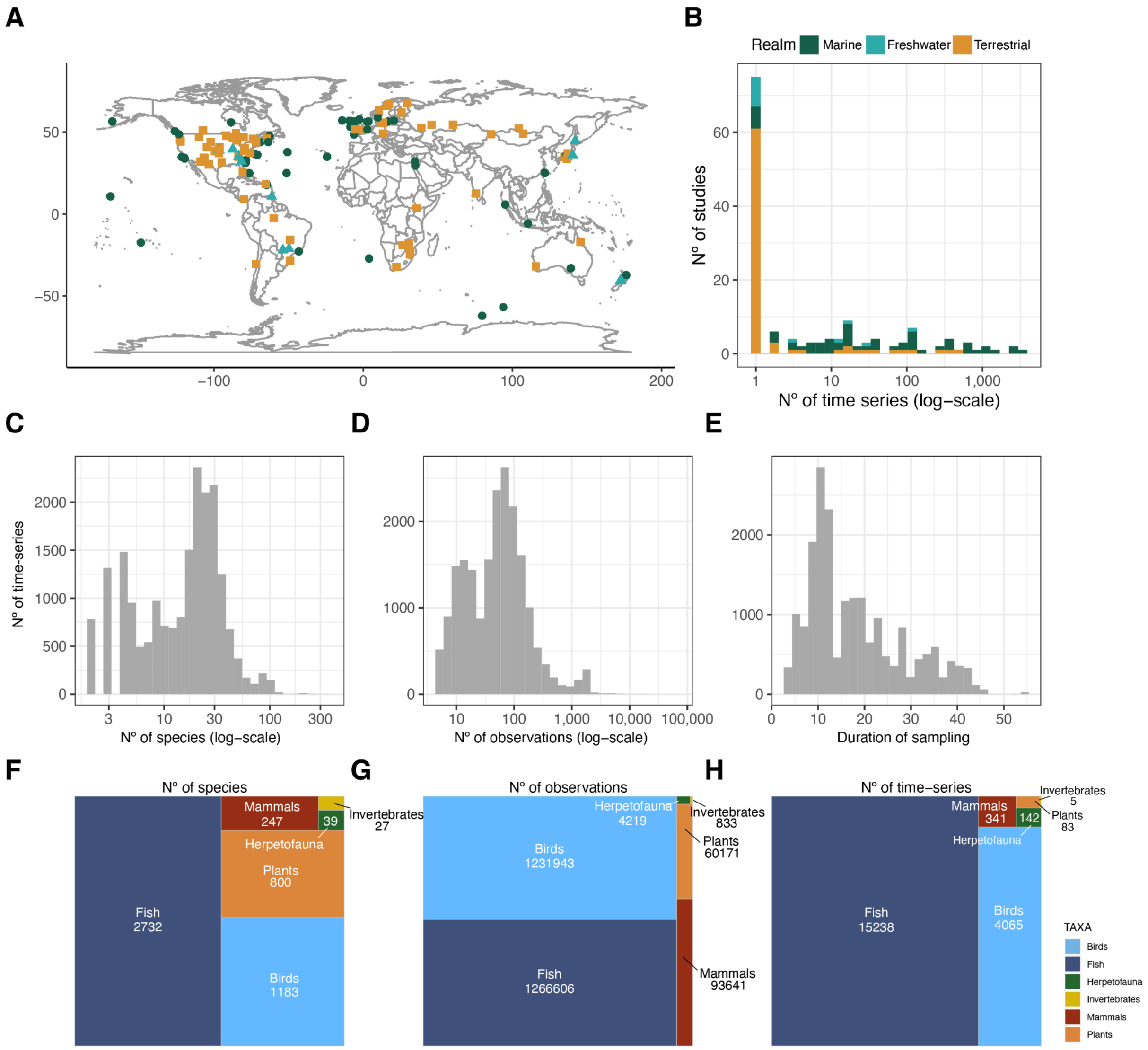

Fig. S2.

Distribution of study data characteristics (BioTIME data, type 2). (A) location of the studies with indirect measures of body size (based on central coordinates; n=151), **(B)** number of assemblage time-series in each study, **(C)** species richness observed across assemblages, **(D)** total number of body size observations across assemblages, **(E)** duration of sampling, and taxonomic distribution of: **(F)** species represented, **(G)** body size observations and **(H)** biodiversity time-series.

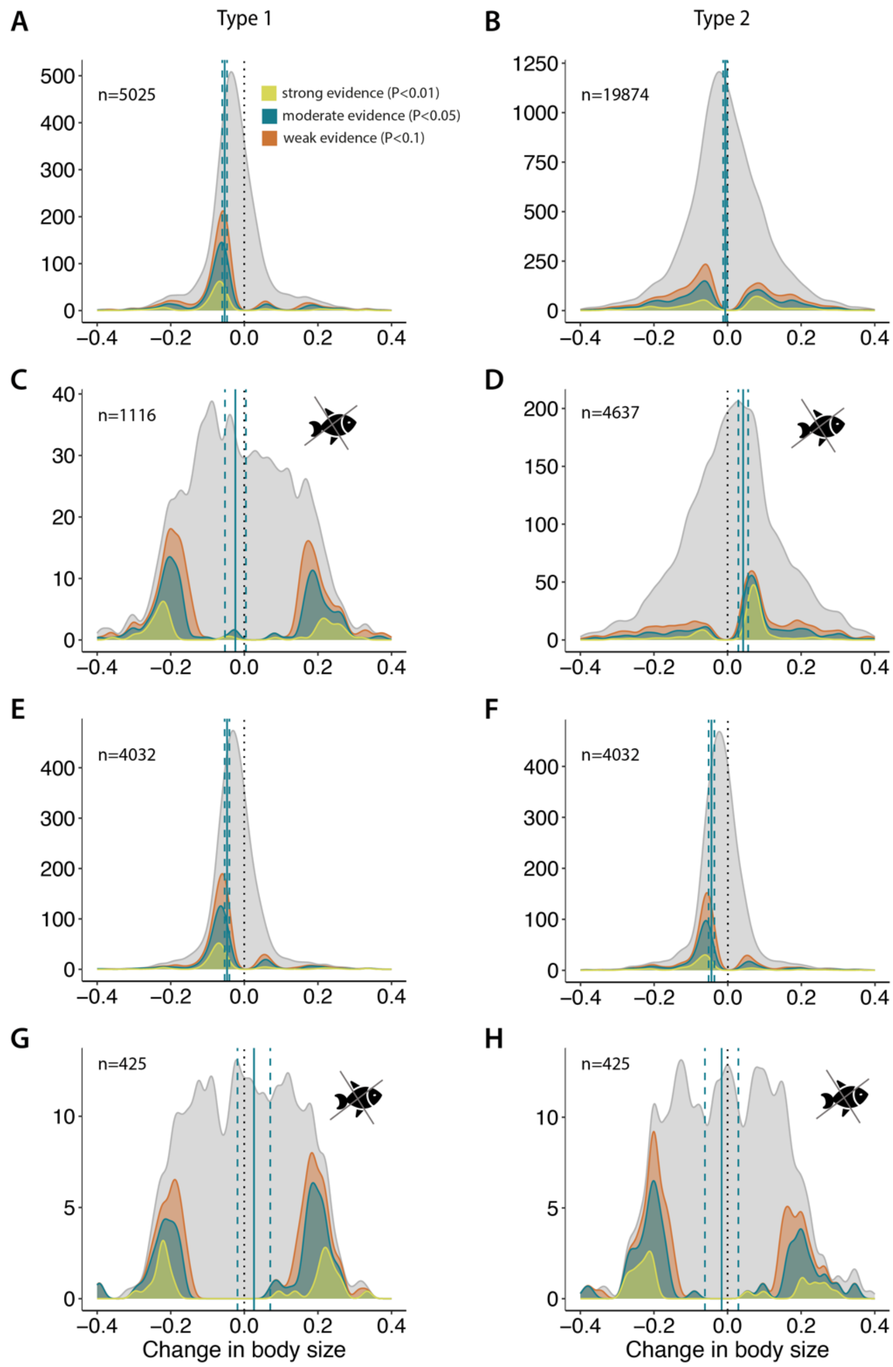

Fig. S3.
Changes in body size across type 1 and type 2 assemblages. The left-hand graphs show the patterns of body size change using direct measures of body size (type 1 data), while the right-hand graphs show patterns using species' average body size estimates from trait databases (type 2 data). **A-B** shows patterns across the full sets of assemblages, and **C-D** when fish assemblages are excluded. **E-F** show changes in body size across common type 1 and type 2 assemblages considering only species where both types of data were available, using either **(E)** direct measures of body size or **(D)** species' average body size estimates; and **G-H** when fish assemblages are excluded.

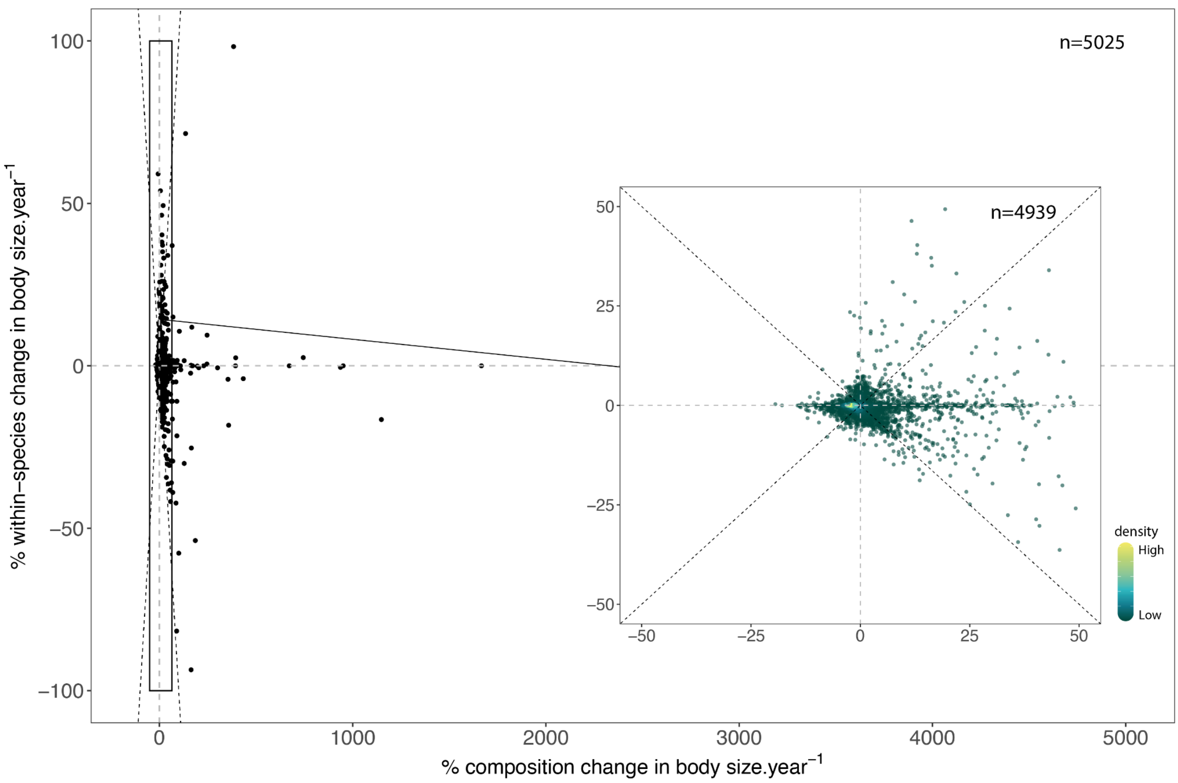

Fig. S4.

Patterns of body size change through time in 5,025 assemblages. Relationship between population-level (i.e., within-species) changes and assemblage-level (i.e., compositional) changes. Both axes show % changes standardised by the number of years between the first and last year sample on the assemblage (duration); assemblages (points) are coloured by density break (colder colours indicating lower densities); Dashed lines show x = 0, y = 0, x = y and y=-x. Please see fig. S7 for more details.

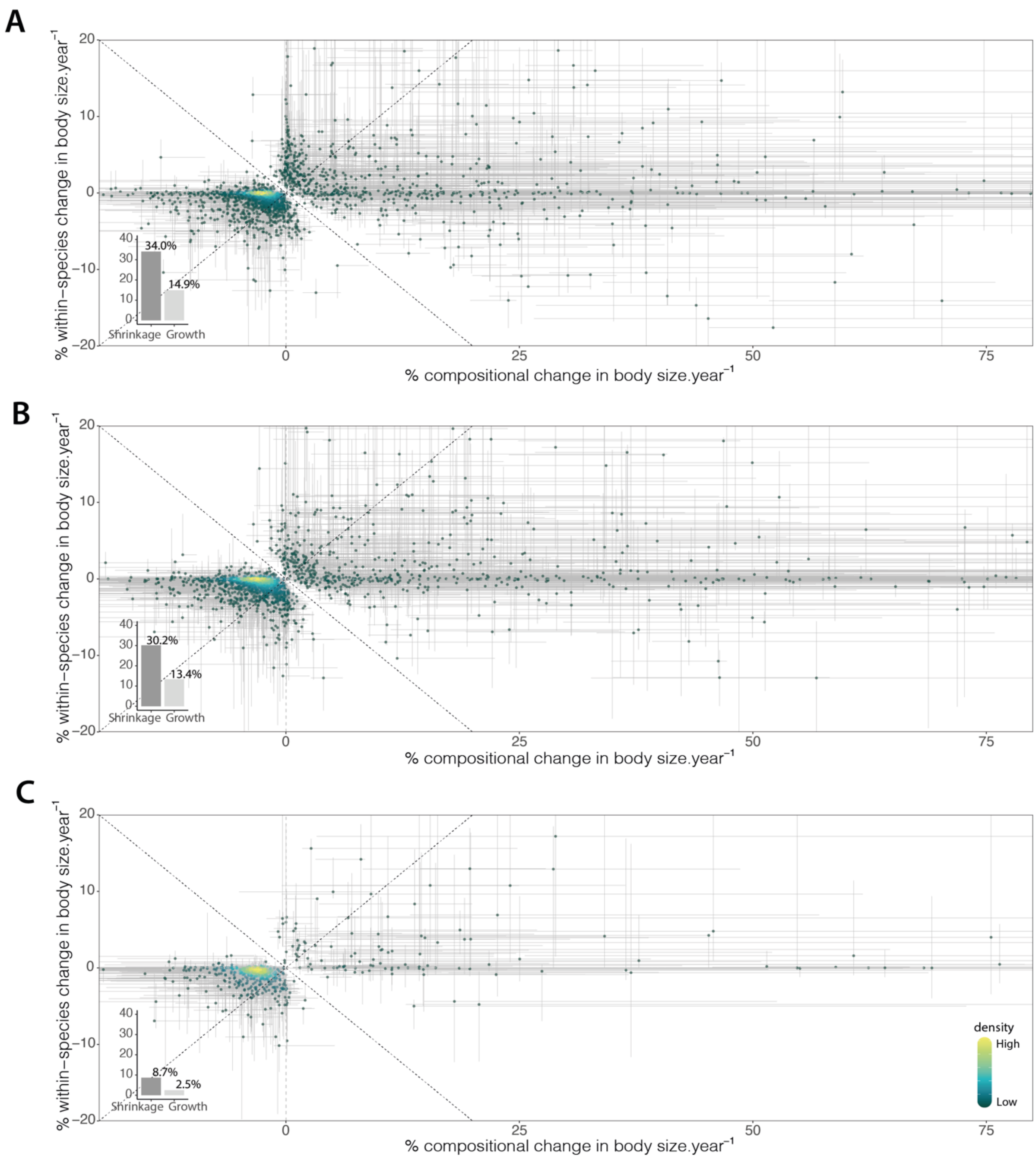

Fig. S5.
Patterns of body size shrinkage through time are not influenced by start and/or end points. Results using alternative start and/or end points. Analysis in the main text only compared the first and the last year of the time-series. The sensitivity analyses used instead an **(A)** fixed start year and random last year, a **(B)** random first year but fixed end year, or a **(C)** random start and end year. Points (assemblages) and grey lines indicate the assemblage median body size change and its IQR across 100 iterations (for each iteration changes were calculated using years chosen randomly according to the scenario assumptions). Points are coloured by density break (colder colours indicating lower densities). Inset histograms show % of assemblage where the median and IQR interval falls below (shrinkage) or above (growth) the y=-x line. Assemblages where the variation (IQR) crosses the y=-x line (and hence neither shrinking nor growing) are not shown.

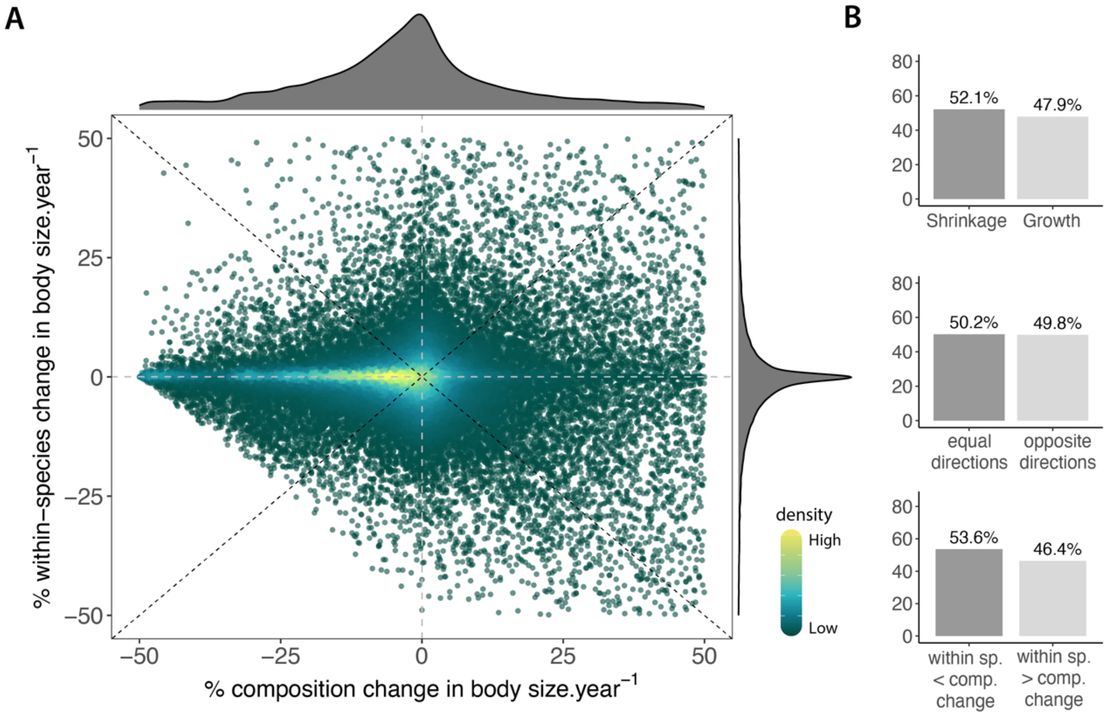

Fig. S6.
Body size change through time between two consecutive years. (A) Partitions for consecutive years across the 5,025 assemblages (n=43,804), where each point represents one pair of consecutive years in a given assemblages (coloured by density break). **(B)** Frequency distributions (in percentage) of the number of pairs in the different scenarios depicted in Fig. 1B. Points with % change year^{-1} higher than 50% are not shown in panel (A), but are included in (B).

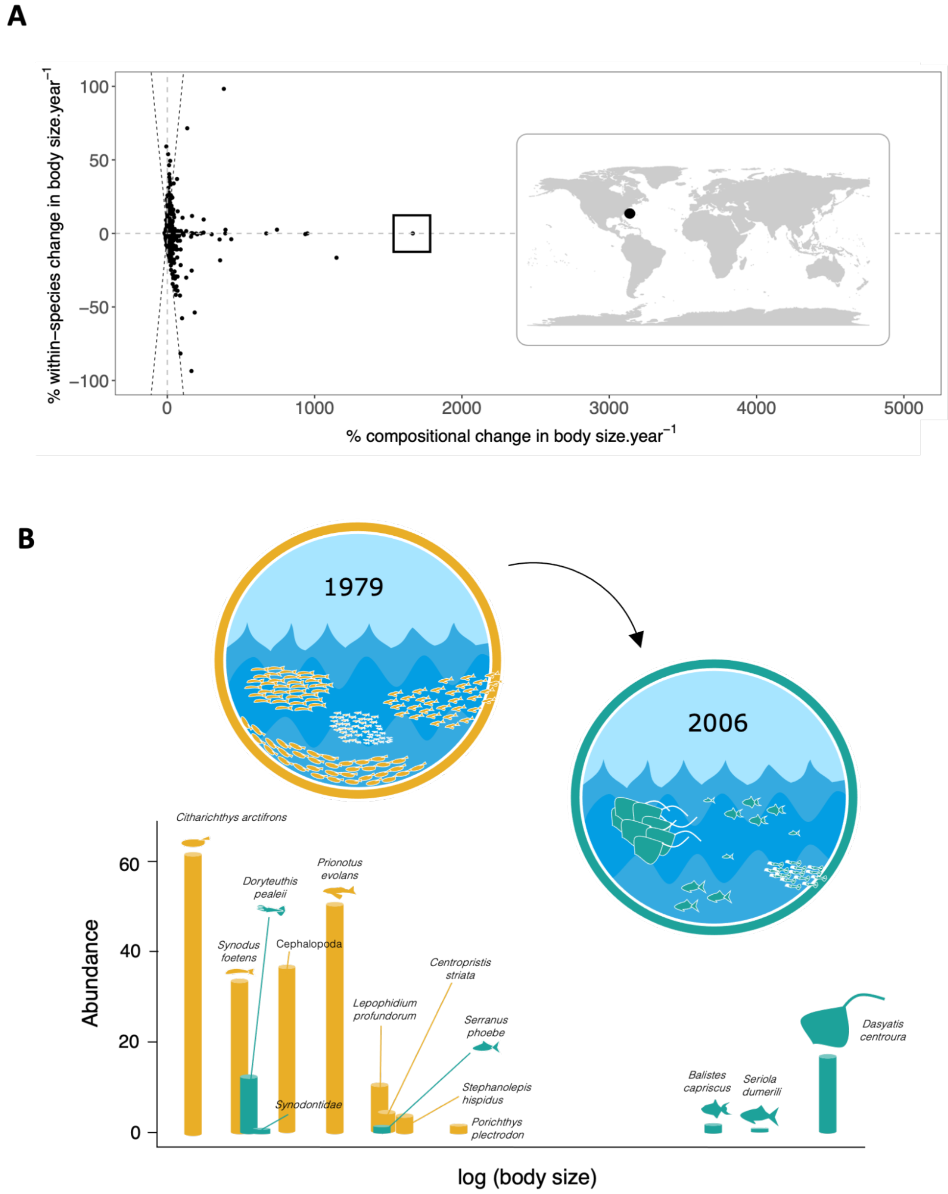

Fig. S7.
Body size change through time: a look into the extremes. The size of the assemblage through time will be determined by changes in species composition and within-species body size changes of each species. More extreme changes can occur in locations where assemblages are composed of species with very different body sizes to begin with, or/and when turnover occurs. For example, in the assemblage highlighted in **(A)** a wide spectrum of benthic organisms was sampled together. **(B)** In the first year (1979; orange), only small benthic organisms were recorded, although in high abundances (CWM_{before}=6.8x10^{-3}), however, by the last year (2006; green) a complete turnover in the assemblage had occurred. Despite decreases in both species' richness and abundance, the size of the assemblage increased (CWM_{after}=3.193), with the addition of several large-bodied species, including several individuals of the genus *Dasyatis*. This led to an assemblage ~467.5 times bigger (in weight) than the original, an increase of ~1666% per year due to compositional changes alone. Note that the illustrations are not to scale, and thus the size of the icons does not represent the real difference between the average body size of the species in the wild.

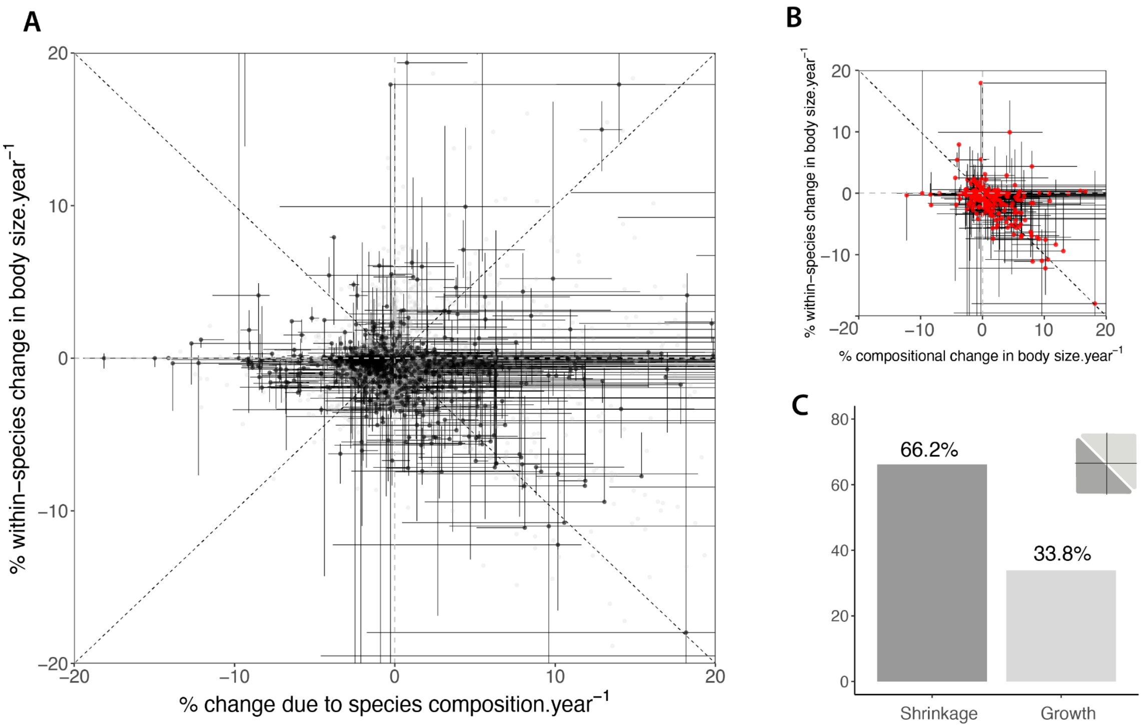

Fig. S8.

Sensitivity analysis using different rarefaction subsets. (A) 20.9% of assemblages (black points; n=1052) are affected by the sample-based rarefaction process. Grey lines indicate the variation (IQR) found in this subset of assemblages across 100 resamples. Assemblages unaffected by this process are shown in grey on the background. **(B)** Assemblages where the variation (IQR) crosses the y=-x line (and hence neither shrinking nor growing; n=365). **(C)** Histograms show % of assemblage where the median and IQR interval falls below (shrinkage) or above (growth) the y=-x line after excluding assemblages highlighted in (**B**). For clarity, assemblages with % change.year^{-1} higher than 20% are not shown in panels (A) and (B), but are included in (C).

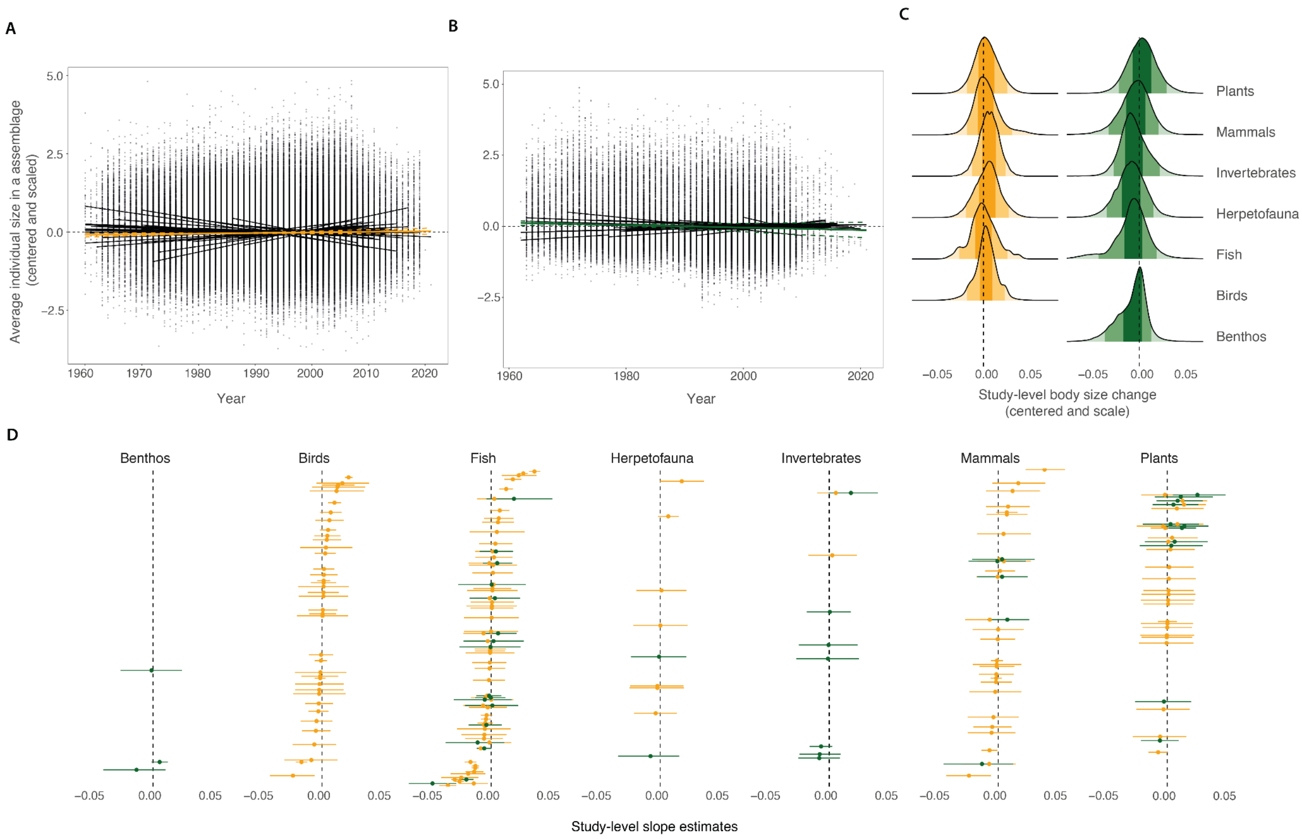

Fig. S9.
Global temporal trend in body size change across assemblages. Overall trend in average individual body size (centred and scaled) change as a function of year when considering **(A)** species' average body size estimates or **(B)** direct measurements of size. Lines depict the global median and 90% credible interval across all assemblages. Black lines show study-level variation. **(C)** Density ridges of posterior distributions of the study-level slope coefficients for a given taxon. **(D)** Estimates of change for each taxon, each point represents a single study, with the bar showing the 90% credible interval; studies are arranged by their median value (point). In all plots, colour represents the type of body size data: orange = average body size from trait databases (20,173 assemblages across 149 studies), dark green = body size from direct measurements as reported in the BioTIME database (5,025 assemblages across 45 studies).

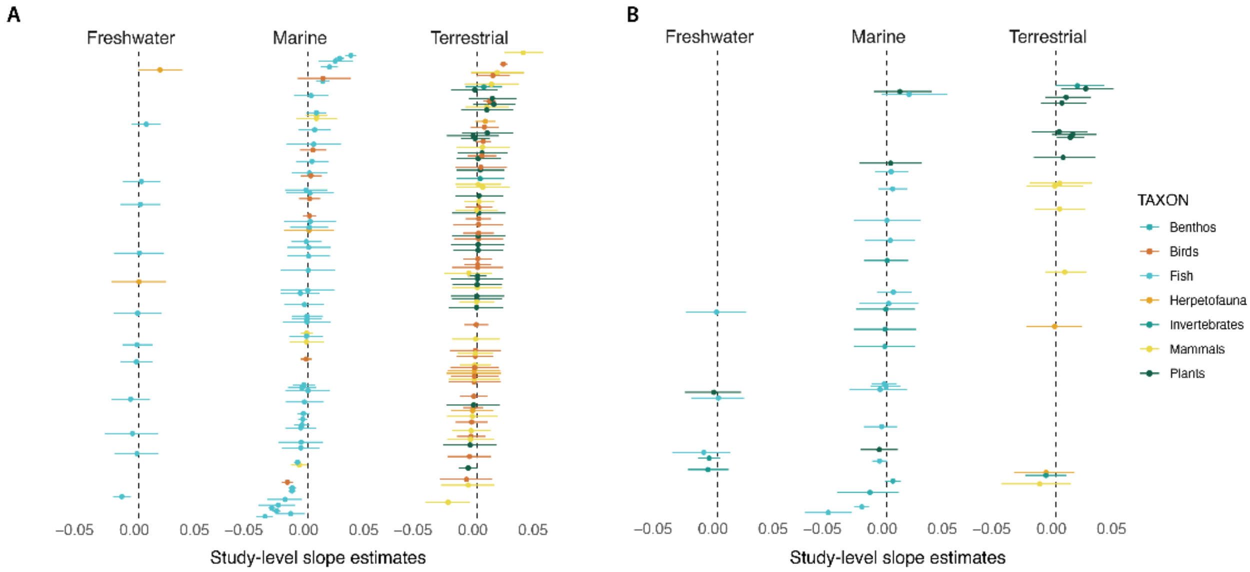

Fig. S10.

Patterns of average individual body size change across the different realms. Estimates of change for each realm when considering **(A)** species' average body size estimates (149 studies) or **(B)** direct measurements of size (45 studies). Each data point represents a single study, with the bar showing the 90% credible interval; studies are arranged by their median change value (point).

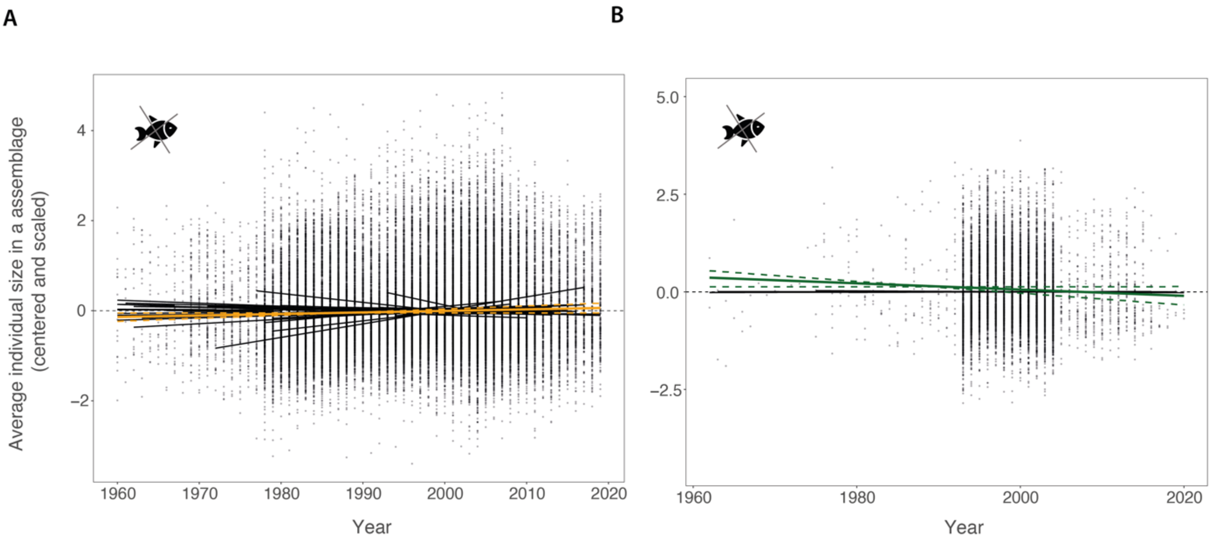

Fig. S11- Same as **fig. S9**, A and B, but when fish are excluded from both datasets.

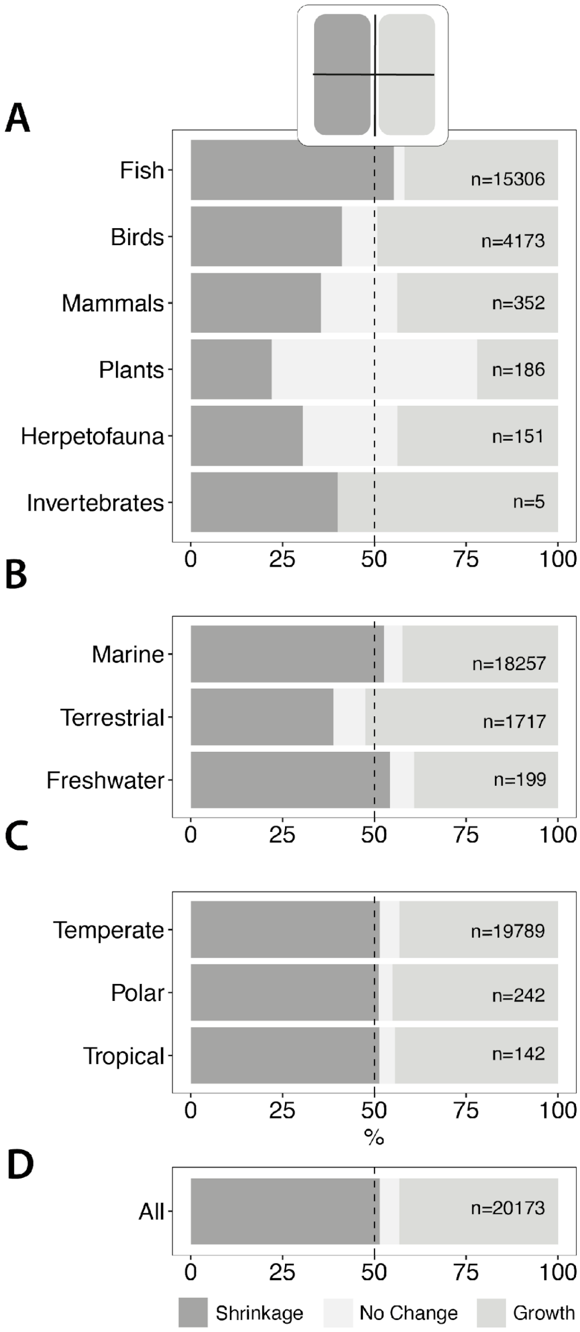

Fig. S12.
Patterns of temporal body size change associated with compositional change alone (type 2 data). Patterns across **(A)** taxa, **(B)** realms, **(C)** climates, and the **(D)** globe as shown in Fig.4. Dashed lines mark the 50% threshold.

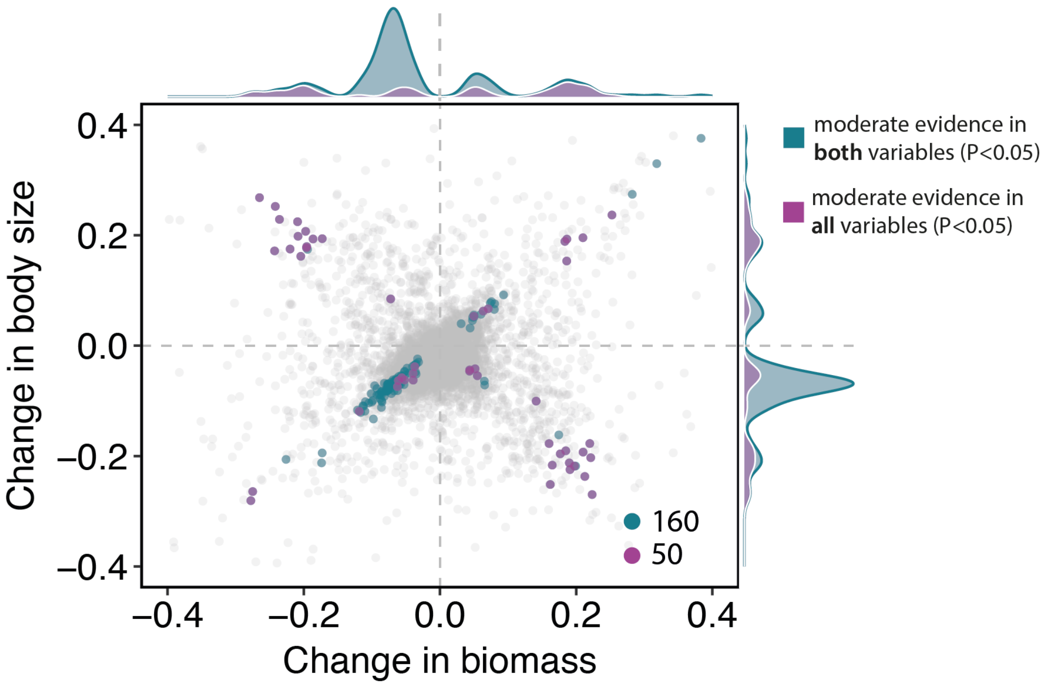

Fig. S13.
Body size change through time as a function of biomass change. Only assemblages for which strong or moderate evidence (P<0.05) was detected for both variables plotted are shown in blue. Purple highlights the assemblages for which significant changes through time were detected in all three variables (n=50), all remaining assemblages are shown in light grey.

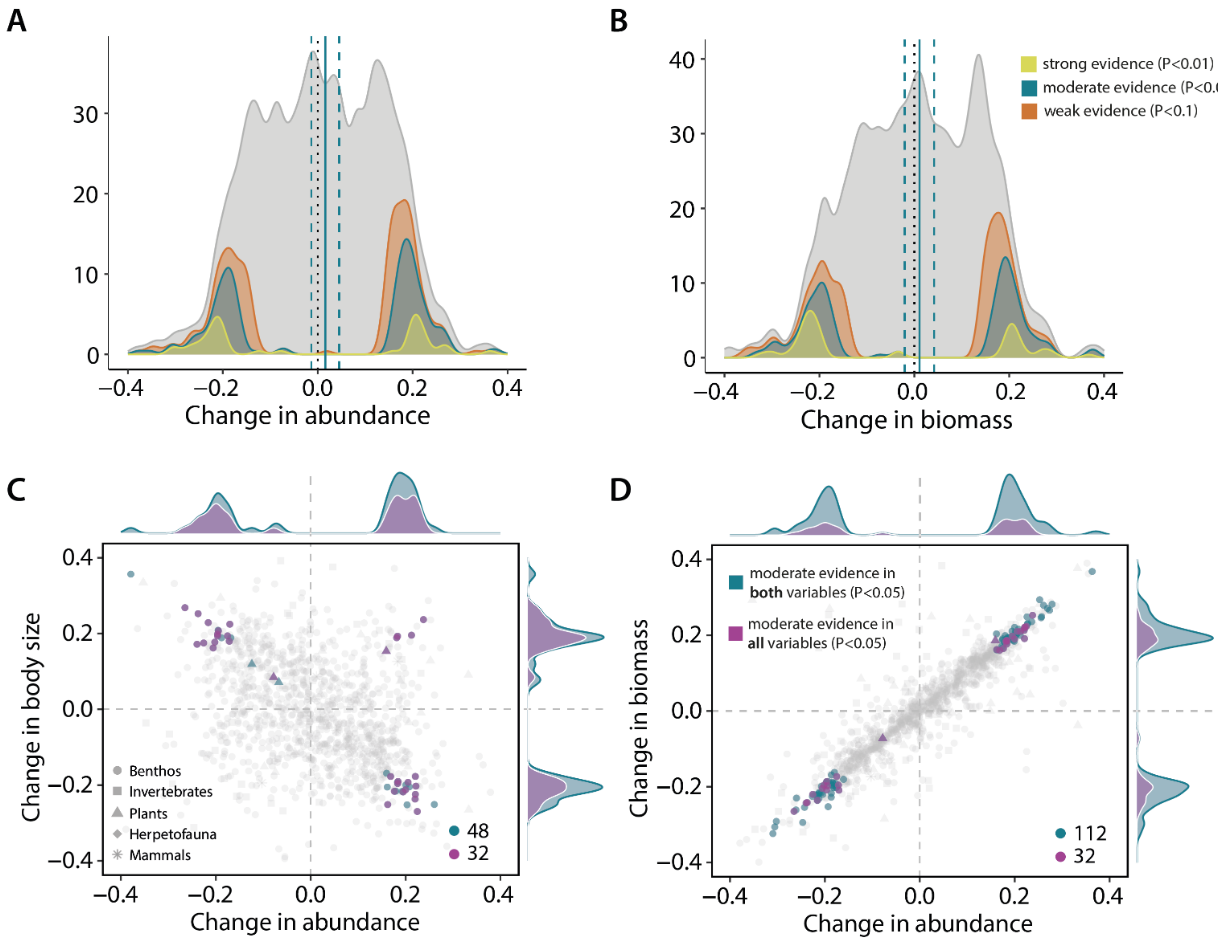

Fig. S14.
Same as **Fig. 5**, but when fish are excluded from the dataset (n=1116). Symbols represent different non-fish taxa.

Table S1. Details on the datasets used in this study.

Study ID	Start year	End year	Nr yrs	Taxon	Realm	Climate	type1	type2	References
39	1970	2015	45	Birds	Terrestrial	Temperate		x	(*57-60*)
42	1960	1979	20	Birds	Terrestrial	Temperate		x	(*61-67*)*
44	1962	1977	16	Plants	Terrestrial	Temperate	x	x	(*68-70*)*
45	2005	2010	5	Fish	Marine	Tropical	x	x	(*71, 72*)
46	1960	1979	20	Birds	Terrestrial	Temperate		x	(*73*)
47	1960	1977	18	Birds	Terrestrial	Temperate		x	(*74*)
51	1964	1977	14	Birds	Terrestrial	Temperate		x	(*75, 76*)
52	1968	1980	13	Mammals	Terrestrial	Polar		x	(*77, 78*)
53	1966	1976	10	Mammals	Terrestrial	Temperate		x	(*79, 80*)
56	1989	2019	31	Mammals	Terrestrial	Temperate	x	x	(*81*)
58	1991	2008	18	Birds	Terrestrial	Tropical		x	(*82, 83*)
59	1977	2002	26	Mammals	Terrestrial	Temperate		x	(*84*)
60	1982	2005	6	Plants	Terrestrial	Tropical		x	(*85-90*)
81	1997	2010	14	Mammals	Marine	Temperate		x	(*91, 92*)
86	1985	2007	16	Plants	Marine	Temperate	x		(*93*)
91	1992	1999	8	Birds	Marine	Temperate		x	(*94*)
100	1981	2011	31	Fish	Marine	Temperate		x	(*95-97*)*
108	1981	2006	25	Birds	Marine	Global		x	(*98*)
112	1973	2005	22	Fish	Marine	Temperate/Tropical		x	(*99*)
119	1970	2010	41	Fish	Marine	Temperate	x	x	(*100*)
121	2000	2010	8	Fish	Marine	Temperate/Tropical		x	(*101*)
123	2000	2009	10	Fish	Marine	Temperate	x	x	(*102*)
125	1988	2000	12	Fish	Marine	Temperate	x	x	(*103*)
126	1974	1980	7	Fish	Marine	Temperate		x	(*104*)
127	1980	1989	10	Fish	Marine	Temperate	x	x	(*105*)
††163	1993	2004	12	Benthos	Marine	Temperate	x		(*106*)
††163	1993	2004	12	Birds	Marine	Temperate		x	
††163	1993	2004	12	Fish	Marine	Temperate		x	
†166	1966	1990	23	Birds	Marine	Global		x	(*107-112*)
†166	1971	1988	13	Mammals	Marine	Global		x	
†169	1987	2006	20	Birds	Marine	Temperate		x	(*113-116*)
†169	1987	2003	7	Fish	Marine	Temperate		x	
†169	1987	2006	20	Mammals	Marine	Temperate		x	
171	1992	2008	17	Mammals	Marine	Temperate/Tropical		x	(*117*)
†172	2000	2009	10	Birds	Marine	Temperate		x	(*118-121*)
†172	1998	2009	12	Mammals	Marine	Temperate		x	
176	1999	2010	12	Invertebrates	Marine	Temperate	x		(*122*)
180	1970	1995	26	Fish	Marine	Polar/Temperate		x	(*123*)
182	1988	2009	22	Fish	Marine	Temperate		x	(*124*)
189	2001	2010	10	Fish	Marine	Tropical		x	(*125*)
190	2001	2010	10	Fish	Marine	Tropical		x	(*126*)
192	1960	1980	19	Mammals	Marine	Polar/Temperate		x	(*127*)
195	1978	2007	30	Birds	Terrestrial	Temperate		x	(*128*)
196	1987	2012	12	Fish	Marine	Temperate		x	(*129*)
197	1985	2013	28	Fish	Marine	Temperate		x	(*130*)*
198	1991	2013	23	Fish	Marine	Temperate		x	(*131*)*
205	2001	2009	8	Fish	Marine	Temperate		x	(*132*)*
206	1993	2008	16	Fish	Marine	Temperate		x	(*133*)*
207	2003	2008	6	Fish	Marine	Temperate		x	(*134*)*
208	1997	2007	11	Fish	Marine	Temperate		x	(*135*)*

209	1987	2010	24	Fish	Marine	Temperate		x	(*136*)*
210	1965	2011	47	Fish	Marine	Temperate		x	(*137*)*
211	1980	1987	8	Fish	Marine	Temperate	x	x	(*138*)
212	1973	1980	8	Fish	Marine	Temperate	x	x	(*139*)
213	1963	2008	46	Fish	Marine	Temperate	x	x	(*140*)
214	1960	2010	46	Plants	Terrestrial	Temperate		x	(*141*)
215	1960	2008	49	Birds	Terrestrial	Temperate/Tropical		x	(*142*)*
216	2001	2005	5	Birds	Terrestrial	Temperate		x	(*143*)
217	1992	2006	14	Birds	Terrestrial	Temperate		x	(*144*)
218	2006	2010	5	Birds	Terrestrial	Temperate		x	(*145*)
219	1995	2011	17	Herpetofauna	Terrestrial	Temperate		x	(*146*)
220	1995	2011	17	Birds	Terrestrial	Temperate		x	(*146*)
229	1988	2013	26	Fish	Freshwater	Temperate		x	(*147*)
†231	2000	2005	6	Fish	Marine	Temperate		x	
†231	2000	2005	6	Herpetofauna	Marine	Temperate		x	(*148*)
†231	2000	2005	6	Plants	Marine	Temperate		x	
232	1975	1999	16	Fish	Marine	Polar/Temperate	x		(*149*)
234	1965	2002	7	Plants	Terrestrial	Temperate	x	x	(*150-156*)
236	1995	2006	12	Fish	Freshwater	Temperate		x	(*157*)
240	2003	2015	13	Plants	Terrestrial	Temperate	x	x	(*158*)
242	1998	2006	7	Plants	Terrestrial	Temperate		x	(*159*)
243	1992	2014	22	Plants	Terrestrial	Temperate	x	x	(*160, 161*)
244	1999	2012	14	Birds	Marine	Temperate		x	(*162*)
246	2000	2014	15	Fish	Marine	Temperate		x	(*163*)
247	1975	2020	46	Invertebrates	Freshwater	Temperate	x		(*164*)
248	2000	2012	13	Plants	Terrestrial	Temperate		x	(*165*)
249	1992	2015	24	Invertebrates	Terrestrial	Temperate		x	(*166*)
252	1978	1989	12	Fish	Marine	Temperate	x	x	(*167*)
254	1995	2018	24	Plants	Freshwater	Temperate	x		(*168*)
255	1989	2007	10	Plants	Terrestrial	Temperate		x	(*169*)
256	1987	2010	24	Fish	Marine	Temperate		x	(*136*)*
271	2000	2014	15	Fish	Marine	Temperate		x	(*170*)
275	2009	2014	6	Herpetofauna	Terrestrial	Temperate	x		(*171*).
277	1979	2008	10	Plants	Terrestrial	Temperate		x	(*68-70*)*
279	1979	2008	10	Plants	Terrestrial	Temperate	x	x	(*68, 69, 172*)*
288	1970	2005	29	Fish	Marine	Temperate		x	(*100*)
295	2008	2016	9	Fish	Marine	Temperate	x	x	(*173*)
296	2008	2016	9	Fish	Marine	Temperate		x	(*173*)
305	1976	1990	15	Herpetofauna	Terrestrial	Temperate		x	(*174*)
308	1980	1998	19	Mammals	Terrestrial	Temperate	x	x	(*175*)
311	1981	2013	33	Mammals	Terrestrial	Temperate		x	(*176*)
312	1961	1984	8	Mammals	Terrestrial	Tropical		x	(*177*)
316	1989	2006	18	Herpetofauna	Terrestrial	Temperate	x		(*178*)
317	1995	2005	9	Plants	Terrestrial	Temperate		x	(*179*)
†318	1994	2009	13	Birds	Terrestrial	Temperate		x	(*180*)*
†318	1994	2009	13	Mammals	Terrestrial	Temperate		x	
319	1990	2003	13	Herpetofauna	Terrestrial	Temperate		x	(*181*)
321	1995	2007	13	Mammals	Terrestrial	Temperate	x	x	(*182*)
324	2003	2007	5	Plants	Terrestrial	Tropical		x	(*183*)
325	2003	2007	5	Plants	Terrestrial	Tropical		x	(*183*)
327	1989	2005	17	Mammals	Terrestrial	Temperate	x	x	(*184*)
328	1979	2008	30	Herpetofauna	Freshwater	Temperate		x	(*185*)
329	1990	2010	6	Plants	Terrestrial	Tropical		x	(*185*)

332	1984	1995	12	Fish	Freshwater	Temperate		x	(*186*)
335	1962	1974	12	Fish	Freshwater	Temperate		x	(*187*)
336	1989	2002	14	Plants	Terrestrial	Temperate		x	(*84*)
339	1960	2009	50	Birds	Terrestrial	Temperate		x	(*188*)
348	2006	2016	10	Mammals	Terrestrial	Temperate/Tropical	x	x	(*189*)
350	1989	2011	12	Benthos	Marine	Temperate	x		(*190, 191*)
351	1989	2004	13	Benthos	Marine	Temperate	x		(*192, 193*)
356	1971	2013	34	Plants	Terrestrial	Tropical		x	(*194*)
357	1994	2006	13	Mammals	Terrestrial	Temperate		x	(*195*)
358	1977	1992	16	Birds	Terrestrial	Temperate		x	(*196*)
359	2000	2012	13	Fish	Marine	Temperate		x	(*197*)
361	1962	1983	22	Birds	Terrestrial	Temperate		x	(*198*)
363	1963	1999	37	Birds	Terrestrial	Temperate		x	(*199*)
365	1997	2002	6	Fish	Marine	Temperate		x	(*200*)
366	1989	2013	25	Mammals	Terrestrial	Temperate		x	(*201*)
372	2005	2013	9	Birds	Terrestrial	Temperate		x	(*202*).
373	2005	2012	8	Mammals	Terrestrial	Temperate		x	(*203*)
374	2004	2014	11	Birds	Marine	Temperate		x	(*204*)
375	2004	2014	11	Invertebrates	Terrestrial	Temperate	x	x	(*205*)
377	2009	2013	5	Birds	Terrestrial	Temperate		x	(*205*)
381	1986	1992	7	Herpetofauna	Terrestrial	Temperate		x	(*206*)
382	1960	1967	8	Mammals	Terrestrial	Temperate		x	(*207, 208*)
402	2010	2015	6	Fish	Freshwater	Tropical		x	(*209*)
403	1989	1995	7	Herpetofauna	Freshwater	Tropical		x	(*210*).
412	1995	2000	6	Fish	Marine	Temperate		x	(*211*)
420	1964	2001	38	Birds	Terrestrial	Polar/Temperate		x	(*212*)
427	1977	2008	32	Invertebrates	Freshwater	Temperate	x		(*213, 214*)
†428	1964	2015	43	Birds	Marine	Temperate		x	(*215-218*)
†428	1960	2015	56	Fish	Marine	Temperate		x	
430	1985	2016	32	Fish	Freshwater	Temperate		x	(*219*)
431	1984	2015	30	Fish	Freshwater	Temperate		x	(*219*)
432	1998	2016	19	Fish	Freshwater	Temperate		x	(*219*)
435	2012	2019	7	Fish	Marine	Polar/Temperate		x	(*220*)
435	2009	2019	11	Invertebrates	Marine	Polar/Temperate	x		
436	2005	2012	5	Fish	Marine	Tropical	x	x	(*221*)
438	2006	2014	7	Fish	Marine	Tropical	x	x	(*222*)
439	1985	1997	13	Birds	Terrestrial	Temperate		x	(*223*)
440	1985	1997	13	Birds	Terrestrial	Temperate		x	(*223*)
441	1985	1997	13	Birds	Terrestrial	Temperate		x	(*223*)
442	1980	1985	6	Birds	Terrestrial	Temperate		x	(*224*)
444	1983	1987	5	Birds	Terrestrial	Temperate		x	(*225*)
446	2007	2011	5	Mammals	Terrestrial	Temperate		x	(*226*)
447	2006	2014	9	Mammals	Terrestrial	Temperate		x	(*227*)
449	2000	2009	10	Mammals	Terrestrial	Temperate		x	(*228*)
464	2007	2011	5	Plants	Terrestrial	Temperate		x	(*229-231*)
465	2007	2012	6	Plants	Terrestrial	Temperate		x	(*229-231*)
466	1986	2008	23	Fish	Marine	Temperate		x	(*232*)
469	1985	2011	27	Fish	Marine	Temperate		x	(*233*)
471	2004	2013	10	Plants	Terrestrial	Temperate		x	(*234*)
475	1960	1972	12	Birds	Terrestrial	Temperate		x	(*235*)
477	1998	2012	15	Invertebrates	Marine	Temperate	x		(*236, 237*)
501	2004	2012	9	Fish	Marine	Temperate		x	(*238*)
502	1962	2009	7	Plants	Terrestrial	Temperate	x	x	(*239*)

504	2003	2007	5	Fish	Marine	Temperate		x	(*240*)
505	1990	2012	11	Fish	Marine	Temperate		x	(*241*)
511	2005	2015	6	Fish	Marine	Tropical	x	x	(*242*)
516	1997	2013	5	Mammals	Terrestrial	Tropical		x	(*243-247*)
521	1972	2017	37	Mammals	Terrestrial	Temperate		x	(*248*)*
522	1987	2013	20	Birds	Terrestrial	Temperate		x	(*249*)*
523	1992	2007	16	Birds	Terrestrial	Temperate		x	(*250*)*
†524	1993	1998	6	Birds	Terrestrial	Tropical		x	(*251*)*
†524	1993	1998	6	Mammals	Terrestrial	Tropical		x	
526	2006	2013	8	Fish	Marine	Temperate		x	(*252*)*
527	2006	2019	14	Birds	Marine	Polar/Temperate		x	(*253*)*
547	2007	2011	5	Plants	Terrestrial	Temperate		x	(*229-231*)
548	2007	2012	6	Plants	Terrestrial	Temperate		x	(*229-231*)
549	2011	2015	5	Fish	Freshwater	Tropical	x	x	(*254, 255*)*
550	2005	2021	17	Fish	Freshwater	Tropical	x	x	(*256*)*
551	1999	2018	19	Fish	Freshwater	Tropical		x	(*257*)*
551	1999	2018	20	Fish	Freshwater	Tropical	x		
552	1963	2010	7	Invertebrates	Terrestrial	Temperate	x		(*258, 259*)*
602	1965	2002	7	Plants	Terrestrial	Temperate	x	x	(*150-156*)*
3541064	2003	2015	13	Plants	Marine	Temperate/Tropical	x		(*260*)
3541065	2008	2014	7	Plants	Marine	Temperate/Tropical	x		(*260*)

Note: † These studies were classified as 'multiple taxa' in the original data sources; †† These studies were classified as 'benthos' in the original data sources. Approximately 83% of these studies are publicly available in the published BioTIME Database (*17*), those remaining are publicly available elsewhere and are indicated by an asterisk.