Synthesis reveals biotic homogenisation and differentiation are both common

Shane A. Blowes[1,2*], Brian McGill[3], Viviana Brambilla[4], Cher F. Y. Chow[4], Thore Engel[1,2], Ada Fontrodona-Eslava[4], Inês S. Martins[4,5], Daniel McGlinn[6], Faye Moyes[4], Alban Sagouis[1,2], Hideyasu Shimadzu[7,8], Roel van Klink[1,2], Wu-Bing Xu[1,2], Nicholas J. Gotelli[9], Anne Magurran[4], Maria Dornelas[4], Jonathan M. Chase[1,2]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig; Leipzig, Germany.

[2]Department of Computer Science, Martin Luther University Halle-Wittenberg; Halle (Saale), Germany.

[3]School of Biology and Ecology and Mitchell Center for Sustainability Solutions, University of Maine; Orono, ME, USA.

[4]Centre for Biological Diversity, School of Biology, University of St Andrews; St Andrews, Scotland.

[5]Leverhulme Centre for Anthropocene Biodiversity, Berrick Saul Second Floor, University of York; York, UK.

[6]Department of Biology, College of Charleston; Charleston, SC, USA.

[7]Department of Mathematical Sciences, Loughborough University; Leicestershire, UK.

[8]Graduate School of Public Health, Teikyo University; Tokyo, Japan.

[9]Department of Biology, University of Vermont; Burlington, VT, USA.

[*]Corresponding author: shane.blowes@idiv.de

Earth's biodiversity continues to change rapidly through the Anthropocene[1], including widespread reordering of species in space[2,3] and time[4,5]. A common expectation of this reordering is that the species composition of sites is becoming increasingly similar across space, known as biotic homogenization, due to anthropogenic pressures and invasive species[6,7]. While many have argued that homogenisationis a common phenomenon (e.g., [6–10]), it is equally plausible that communities can become more different through time, known as differentiation, including through human impacts[11,12]. Here, we used a novel adaptation of Whittaker's (1960)[13] spatial-scale explicit diversity partition to assess the prevalence of biotic homogenisation and differentiation, and associated changes in species richness at smaller and larger spatial scales. We applied this approach to a compilation of species assemblages from 205 metacommunities that were surveyed for 10-64 years, and 54 'checklists' that spanned 50-500+ years. Scale-dependent changes of species richness were highly heterogeneous, with approximately equal evidence for homogenisation(i.e., lower β-diversity) and differentiation (i.e., higher β-diversity)

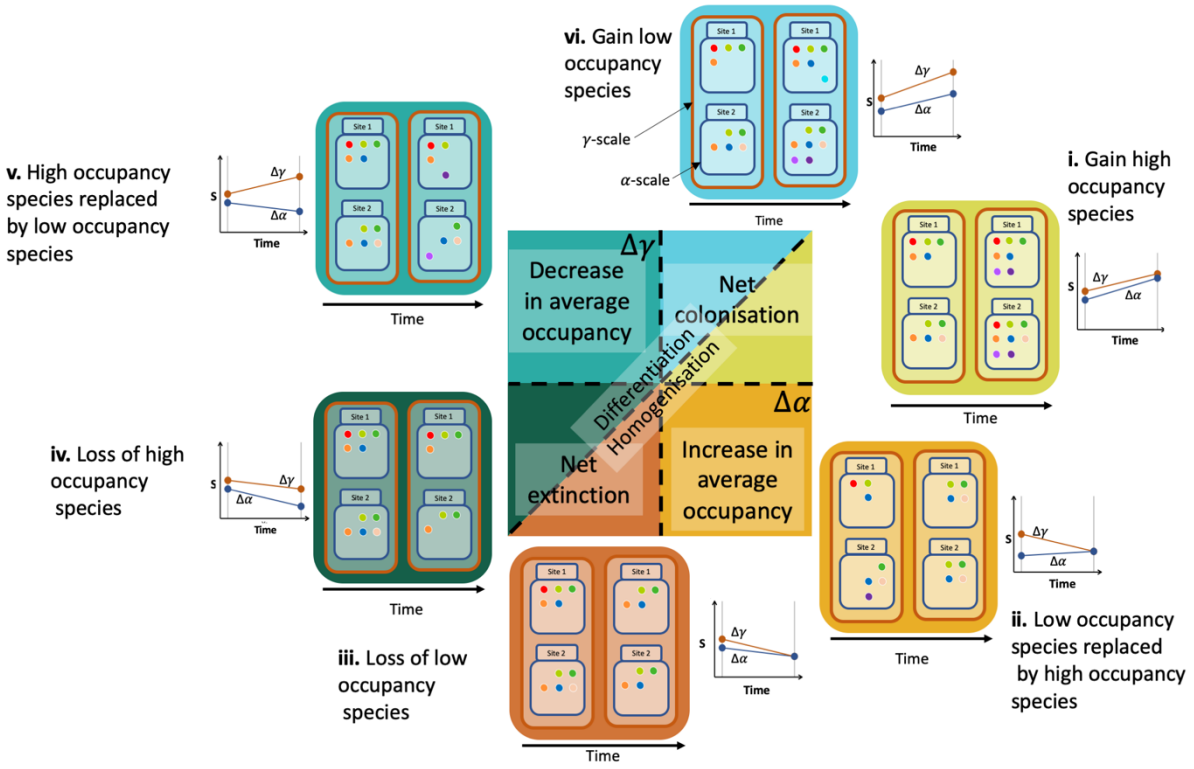
through time across all regions, taxa and data types. Homogenisation was most often due to increased numbers of widespread species, which tended to increase both local and regional richness through time. These results emphasise that an explicit consideration of spatial scale is needed to fully understand biodiversity change in the Anthropocene.

Humans are fundamentally altering the Earth's climate, water and nutrient cycles, and are appropriating over 50% of the Earth's terrestrial net primary production[14]. With this increasing human footprint, consequent changes in Earth's biodiversity are inevitable. There is substantial evidence that humans are accelerating the global extinction rate[15]. However, diversity declines at local scales have not been prevalent, with several syntheses indicating little directional trends amidst substantial variability[4,5,16,17], though not without controversy[18]. It has also been proposed that spatially distinct locations are becoming more similar to one another in species composition through time, commonly called biotic homogenization[6,7]. Homogenisationcan occur, for example, when widespread species replace rare species through mechanisms such as introduction of invasive species, loss of rare species, and homogenisation of landscapes via anthropogenic pressures (e.g., agricultural practices or urbanisation). While homogenisation is frequently reported in empirical studies[8–10,19], it is not clear how common it is relative to other types of scale-explicit biodiversity change[12]. For example, the opposite of biotic homogenization, known as biotic differentiation, can occur when landscapes are fragmented or otherwise made more heterogeneous via human activities, or when exotic species are introduced but do not become widespread[11,12,20]. A comprehensive empirical assessment of the relative frequency of homogenisation, differentiation, or no directional change is lacking.

Change in spatial differentiation of community composition is logically equivalent to differential rates of change in diversity at two spatial scales[11,12]. This can be clearly seen with Whittaker's (1960)[13] diversity partition where the diversity of a single site is α-diversity and the sum of the diversity of several local sites (i.e., a region) is γ-diversity. Variation in local community composition is referred to as β-diversity, and given by: $\beta = \gamma/\bar{\alpha}$ (where $\bar{\alpha}$ is the average local diversity across sites in a region). Whenever rates of change in α- and γ-diversity are not equal through time, there will be some change in β-diversity. Here, we adapt Whittaker's framework such that change in β-diversity emerges naturally when changes at α- and γ-scales are considered jointly (Figure 1). Moreover, these changes in β-diversity can be mathematically linked to changes in the number of sites species occupy. Average occupancy,

or the fraction of sites within a region occupied by species i (o_i), is related to Whittaker's formula by $\beta = \gamma/\bar{\alpha} = \gamma/(\Sigma o_i) = \gamma/(\gamma\bar{o}) = 1/\bar{o}$ [21]. This allows us to connect α- and γ-diversity change with changes in β-diversity and the underlying processes of colonisation and extinction that drive changes in average occupancy.

Six qualitatively distinct scenarios emerge in the intersecting space of changing α- and γ-diversity (Figure 1). The 1:1 line (i.e., $\Delta\gamma = \Delta\alpha$) represents equal log-proportional changes at both scales (i.e. $\log[\gamma_{t2}/\gamma_{t1}] = \log[\alpha_{t2}/\alpha_{t1}]$), and delineates the boundary between homogenisation and differentiation (Figure 1). When $\Delta\alpha > \Delta\gamma$ (i.e., below the 1:1 line), homogenisation occurs. One such scenario involves α-diversity increasing proportionately more than γ-diversity increases via increase of high occupancy species (Figure 1i). Increases in high occupancy species can accompany anthropogenic changes that favour widespread, generalist and/or non-native species. Another scenario involves widespread species replacing low occupancy species causing average occupancy increases and thus homogenisation which would be associated with α-diversity increases, but γ-diversity decreases (Figure 1ii). However, homogenisation can also accompany simultaneously decreasing α- and γ-diversity, as would occur when low occupancy species, such as endemic species or those restricted to only a few sites, go regionally extinct, for example, due to habitat loss or degradation (Figure 1iii). These distinct scenarios all describe decreasing β-diversity and biotic homogenisation, but the outcomes for α- and γ-diversity, and the implications for policy and conservation, are very different. Parallel distinct scenarios of differentiation are also possible. If increasing habitat heterogeneity results in fewer widespread or high occupancy species, increased β-diversity would be associated with lower α- and γ-diversity (Figure 1iv). Increased habitat heterogeneity could also lead to increases in γ-diversity, accompanied by either α-diversity declines (Figure 1v) or increases (Figure 1vi).



98

99 **Figure 1**: **Mechanisms that underpin spatial changes in spatial differentiation in**
100 **composition can be understood by examining the relationship between changes in**
101 **regional- and local-scale species richness through time.** When richness changes at regional
102 ($\Delta\gamma$) and local ($\Delta\alpha$) scales are calculated as proportional changes, assemblages below the
103 dashed 1:1 line, i.e., $\Delta\gamma < \Delta\alpha$, are being homogenised, and β-diversity is decreasing.
104 Conversely, assemblages above the diagonal dashed 1:1 line, i.e., $\Delta\gamma > \Delta\alpha$, are differentiating,
105 and β-diversity is increasing. These changes can be linked to changes in species occupancy,
106 for regions where **(i)** $\Delta\gamma < \Delta\alpha$, and $\Delta\gamma > 0$, $\Delta\alpha > 0$, the number of species with high occupancy
107 (i.e., that occupy the majority of sites in the region) is increasing; **(ii)** $\Delta\gamma < \Delta\alpha$, $\Delta\gamma < 0$ and $\Delta\alpha$
108 > 0, average occupancy is increasing, e.g., due to species with low occupancy being replaced
109 by those with high occupancy; **(iii)** $\Delta\gamma < \Delta\alpha$ and $\Delta\gamma$, $\Delta\alpha < 0$, the number of species with low
110 occupancy is decreasing; **(iv)** $\Delta\gamma > \Delta\alpha$ and $\Delta\gamma$, $\Delta\alpha < 0$, the number of species with high
111 occupancy is decreasing; **(v)** $\Delta\gamma > \Delta\alpha$, $\Delta\gamma > 0$ and $\Delta\alpha < 0$, species with low occupancy (i.e.,
112 occupy few sites in the region) are replacing those with high occupancy; **(vi)** $\Delta\gamma > \Delta\alpha$ and $\Delta\gamma$,
113 $\Delta\alpha > 0$, the number of species with low occupancy (i.e., occupy relatively few sites in the
114 region) is increasing.

115

116 Here, we use the framework of Figure 1 to: i) estimate the overall change in β-diversity
117 (above or below the 1:1 line) observed in empirical studies, and ii) classify changes in β-

diversity into six distinct scenarios. To do so, we required data that recorded species richness at a minimum of two time points across multiple locations. First, we compiled a total of 205 studies that had data on species abundances (or occurrences) through time from at least four locations and at least ten years between the first and last samples. One hundred and thirty-eight of these studies came from already published compiled databases (e.g., [22–24]) and 67 datasets had a similar structure (e.g., species abundances from samples through time), but were not included in these previous compilations and are compiled for the first time here. Second, we used 54 studies that were based on 'checklists' where species occurrence was recorded for sites at historical and contemporary time periods. We chose to include species checklist data here despite their coarse nature, as they have made key contributions to our understanding of long-term trends in introductions and extinctions[25,26], as well biotic homogenisation[27,28]. We analysed whether these distinct data types affected the results.

In total, our analysis on 259 datasets with a total of 16,359 locations is the largest compilation of data sources, ecosystem types, and taxon groups used to examine the question of changes in β-diversity through time to date (Extended Data Figure 1). We estimated temporal changes in species richness for every dataset at the smaller, α-scale, where a sample was taken, and a larger γ-scale, where richness was estimated as the sum of species in all of the local samples. The grain of the α-scale and extent of γ-scales varied among datasets; ranging, for example, from quadrat samples of plant communities collected over small spatial extents ($< 1 km^2$) to species checklists of birds on islands distributed across several oceans. For both the α- and γ-scales, we quantified change through time as the log-ratio of species richness in the most recent time point over the species richness in the initial sample for every location (for α-diversity) or the sum of all locations (for γ-diversity) within each dataset, and then divided that by the number of years between the two samples to get a standardised annual rate of change independent of time series length. We then fit a multilevel model for each scale that estimated the average change occurring (i.e., a non-varying intercept only), which also included a random term for variation between datasets (i.e., varying intercepts). For results presented in the main text, species richness in the initial and final time point were calculated using a single year. However, we repeated all analyses using multiple years to estimate the average richness for two periods (data permitting) so as to verify that starting or ending periods were not having undue influence, and found that results were qualitatively consistent (see Materials and Methods and Extended Data Figure 2).

Overall across datasets, we found many instances for each of the six scenarios identified in Figure 1 (Figure 2a, 2b). Averaged over the entire data set, β-diversity change showed a weak trend towards homogenisation but with the 90% credible interval for this trend clearly overlapping an average β-diversity change of zero (Figure 2c). The weak trend (-0.001) is the equivalent of the loss per decade of 1 out of 100 entirely distinct (i.e., no shared species) communities[29]. Moreover, few individual datasets showed strong evidence for changes in β-diversity in either direction (Figure 2f). Qualitatively, when we count the number of empirical estimates that fall into each outcome, the commonly hypothesised homogenisation scenario[6,7] of high occupancy species causing extinction and replacement of low occupancy species and a concomitant decline in regional diversity is among the least frequent pathways (sector ii in Figure 2b). Where differentiation is occurring (i.e., increases of β-diversity through time), the prevalence of increases in both α- and γ-diversity (sector vi) were approximately balanced by declines at both scales (sector iv in Figure 2b). A common scenario is increases in diversity at both the local and regional scale (sectors i and vi), with small changes in average occupancy (i.e., increasing or decreasing) tipping a given system towards homogenisation or differentiation.

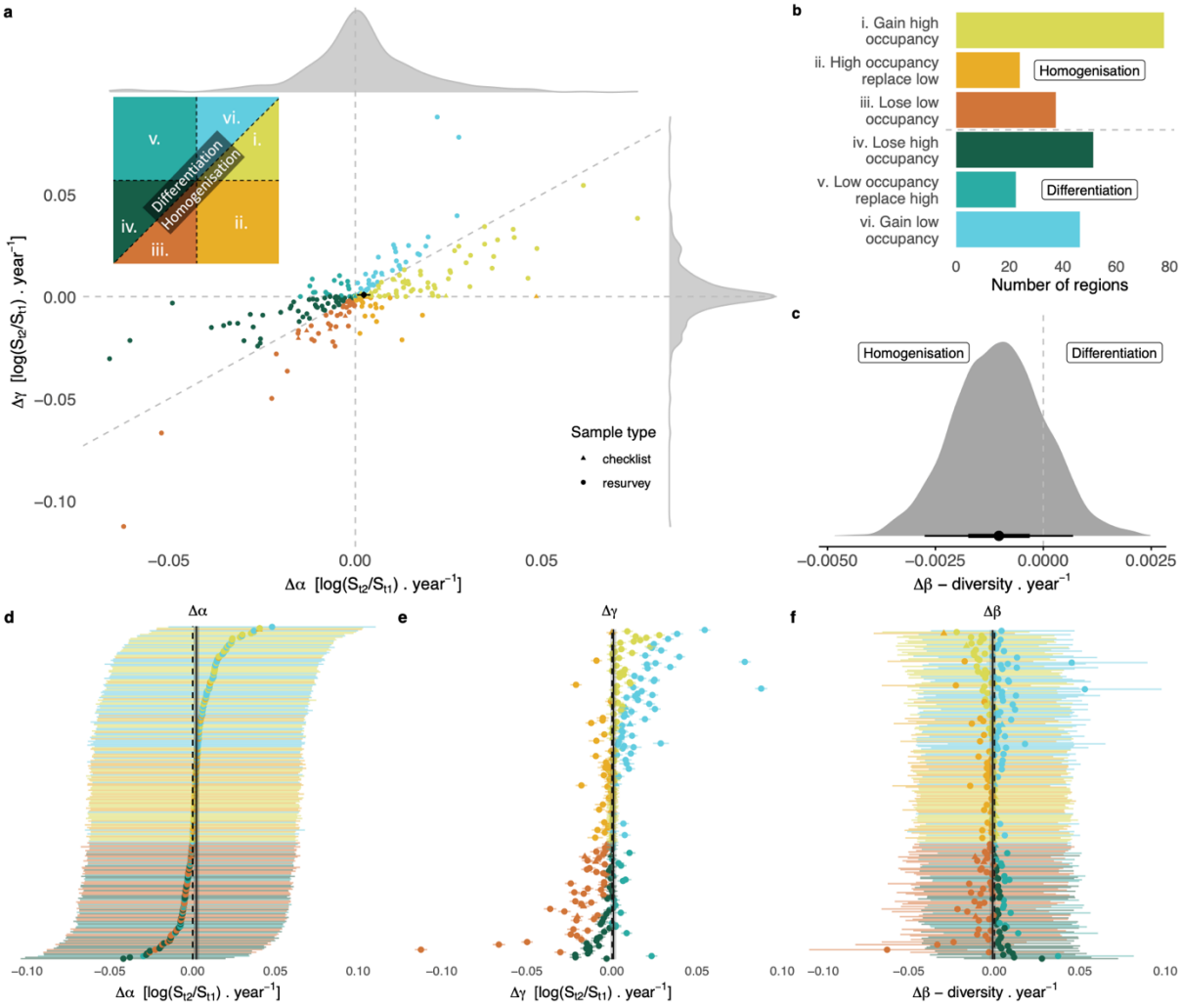


Figure 2: Patterns of homogenisation and differentiation are approximately balanced at the global scale. (a) Empirical estimates of γ-scale changes as a function of α-scale changes, both axes show log-ratios standardised by the number of years between the estimates; the black point shows the γ- and α-scale intercepts and the 90% credible interval from multi-level models fit separately to these data at each scale; colour represents categories of change from Figure 1, shape represents sample type (circle = resurvey, triangles = checklist). Dashed lines show x = 0, y = 0, and x = y. (b) Count of the number of regions in each of the different qualitative outcomes depicted on Figure 1. (c) Kernel density plot of change in β-diversity per year calculated as the distance from 1:1 line (left = homogenisation, right = differentiation) of 1000 draws of α- and γ-scale intercept posterior distributions; black point shows median, bar represents 50% (thick) and 90% (thin) credible intervals. Estimates of change for each region at the (d) α-, (e) γ-, and (f) β-scales; each point represents a single region, with the bar showing the 90% credible interval; regions are in the same order on panels d-f, arranged by the magnitude of the α-scale estimate.

We detected the strongest signature of biotic homogenisation in the freshwater realm, and this was primarily driven by increased average occupancy (i.e., increases in α-diversity and a weaker decrease in γ-diversity; Figure 3a). This is not unexpected since freshwater systems are often regarded as among the most low-connectivity, dispersal-limited ecological systems[30,31]. Indeed, human introductions of non-native species in lakes and rivers are among the most well-known examples of biotic homogenisation (e.g., [32–35]). Homogenisation and differentiation were approximately balanced among terrestrial assemblages (Figure 3a), and associated with weak gains in species richness that did not differ from zero at α- and γ-scales. In contrast, we found that there was a slight tendency towards differentiation in the marine realm (Figure 3a), which was associated with gains in γ-diversity. One possible reason for this is that marine assemblages are typically highly fluid and dynamic, with high connectivity across locations, which might allow species favoured by global change conditions to colonise new regions more readily than in the other realms. Across latitudinal bands (Figure 3b), tropical, subtropical and temperate latitudes showed a trend towards homogenisation driven by relatively large gains in α-diversity, while polar regions showed a trend to differentiation driven by gains in γ-diversity with comparatively small changes in α-diversity, though confidence intervals overlapped no change and sample sizes were small. Data type (resurvey vs checklist), and spatial and temporal scale did not show substantial effects on our results (Figure 3c, Extended Data Figure 2), although larger spatial and temporal scales, including checklist data, were slightly more likely to show homogenisation. Lastly, across taxa, mammals tended towards differentiation driven by declines in α-diversity that were proportionately larger than declines in γ-diversity, while fish tended towards homogenisation due to small γ-scale richness increases of high occupancy species (Figure 3d). As 55/80 fish studies were from freshwater, this parallels our findings for the freshwater realm. But again, β-diversity effect sizes by taxonomic group, latitudinal band, and realm were small and confidence intervals all overlapped with no change with the exception of the freshwater realm (Figure 3).

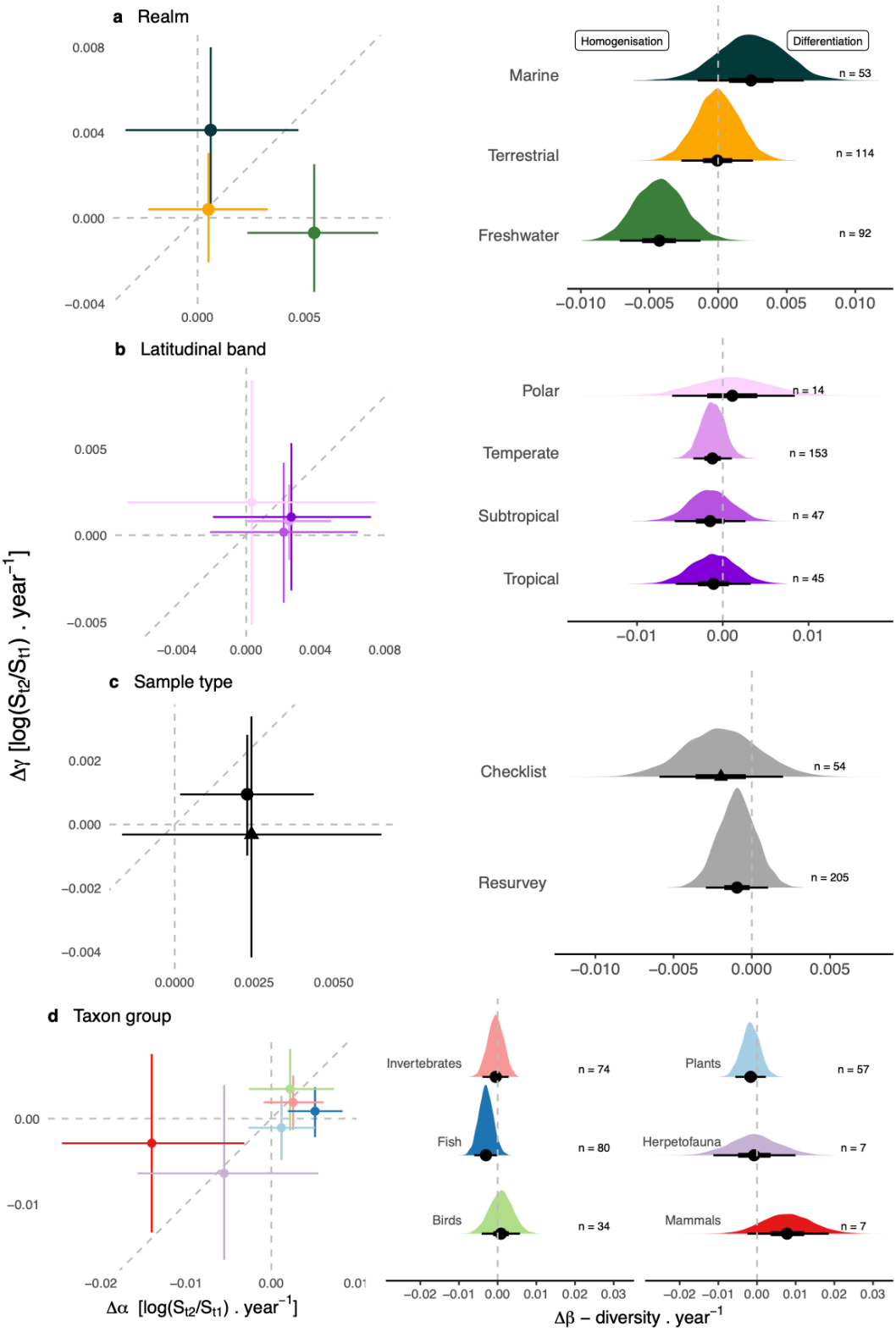


Figure 3: α- and γ-scale species richness changes, and patterns of homogenisation and differentiation varied among sample types, realms, latitudinal bands and taxon groups. γ-scale estimates of the log-ratio as a function of α-scale estimates (left) and distance from 1:1 line (right) for comparisons between (**a**) realms, (**b**) latitudinal bands, (**c**) sample types: checklists and resurveys; and (**d**) taxon groups. Distances from the 1:1 line were calculated using 1000 draws from posterior distributions, where each x,y coordinate was a single draw

215 from the population-level (fixed effect) parameters of α- and γ-scale models, respectively.
216 Points and whiskers show median, 50 and 90% credible intervals.

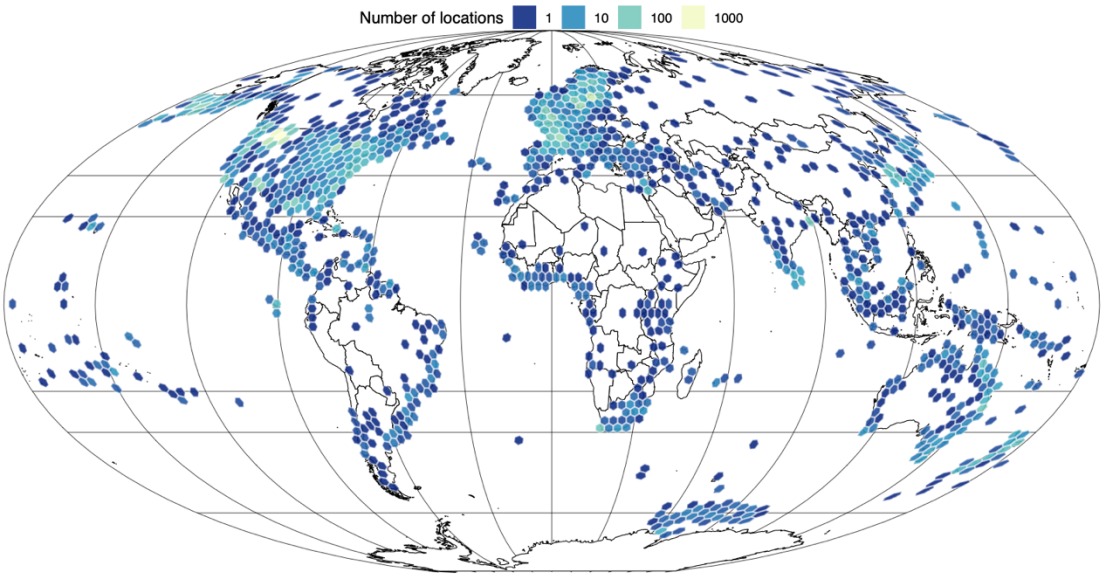
217

218 Our results suggest that β-diversity trends show considerable variability across locations,
219 taxa, and time, with differentiation slightly less likely than homogenisation. This matches
220 findings on local diversity[4,5,16], and population trends[36], where variation in the direction of
221 change means that the strength of overall net trends up or down are weak, and most often
222 statistically indistinguishable from zero. This should not be surprising. While humans are
223 having many impacts that could lead to homogenisation including transporting species and
224 recreating urban or high intensity agricultural landscapes repeatedly, many other impacts
225 could lead to differentiation, including: substantial fragmentation of the landscape, the
226 creation of strong spatial gradients of human impact intensity, applying spatially varying
227 resource management practices and land use regulations, and causing climate change, which
228 induces species to shift at different rates, all leading to spatial heterogeneity[11,37]. In this
229 context, we stress that the lack of prevalence of homogenisation should not in any way be
230 taken to indicate that humans are not having a large impact on biodiversity. Changes in β-
231 diversity either negatively, as in homogenisation, or positively, as in differentiation, are likely
232 often a result of humans modifying nature.

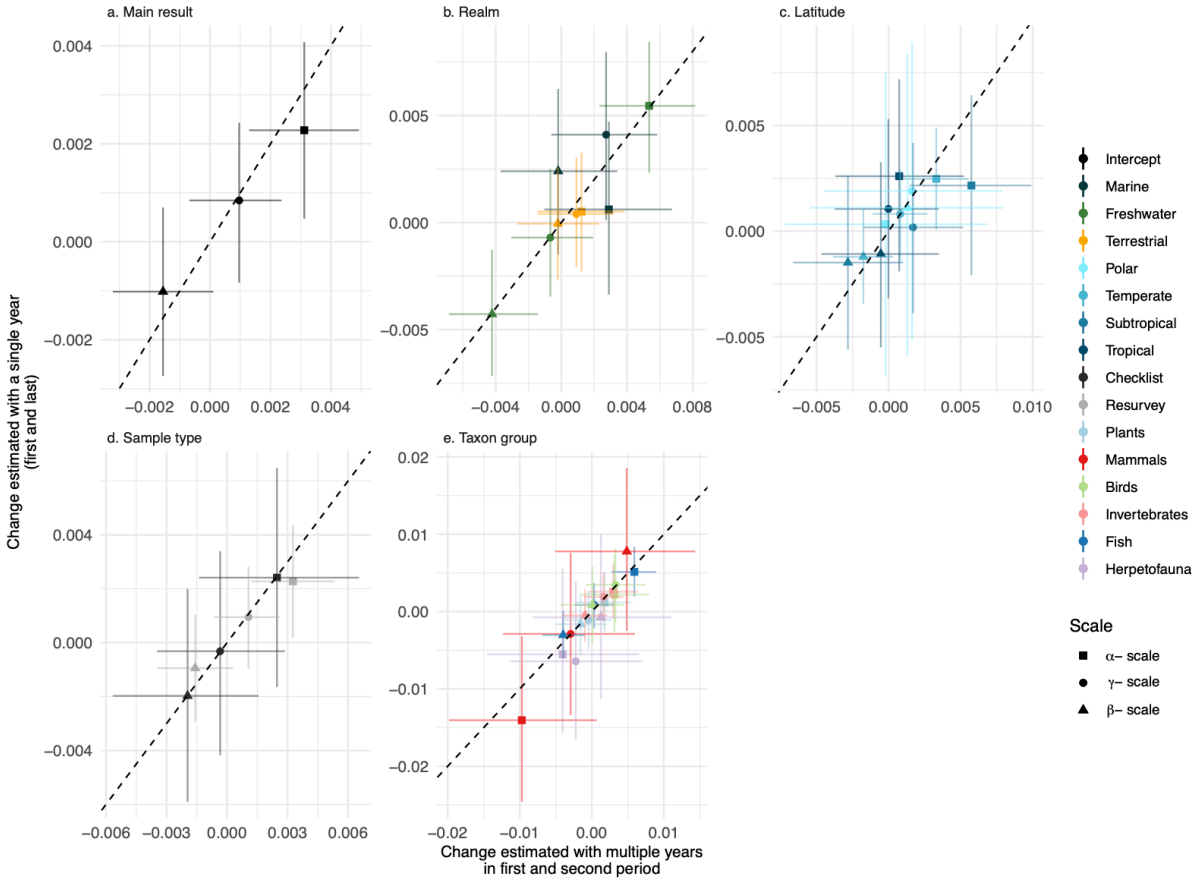
233 Most published tests of the frequency of homogenisation use pairwise comparisons of sites
234 and then averages across all possible pairs, and thus only addresses the α-scale, but not
235 changes at the γ-scale. For example, previous tests of biotic homogenisation concluding that
236 homogenisation was driven by loss of rare species used pairwise averages that are only able to
237 capture single site extirpations, not landscape or regional scale extinctions, and thus can
238 exaggerate the perception of loss. We found that the hypothesised mechanism of widespread
239 species, like invasive species, replacing locally rare species (orange sector ii in Figure 1) is
240 among the rarest pathways of spatial homogenisation. Similarly, efforts to use β-diversity to
241 link changes at local scales (e.g., [5]) to regional or global scale changes (e.g., [38]) also cannot be
242 based on pairwise metrics, which have no representation of the larger scale. Although
243 Whittaker's β-diversity measures and pairwise β-diversity measures (e.g., 1-Jaccard's index)
244 are equivalent for two sites, the two metrics can give very different answers when more than
245 two sites are examined[39,40]. Thus, it is essential to directly estimate changes at each of smaller
246 and larger scales, rather than relying on pairwise similarity metrics that can give misleading
247 answers to how γ-diversity might change through time. For all of these reasons, we believe

that using a perspective based on the Whittaker diversity partition, combined with the new classification we propose, provides a more accurate and constructive way of measuring β-diversity to inform policy.

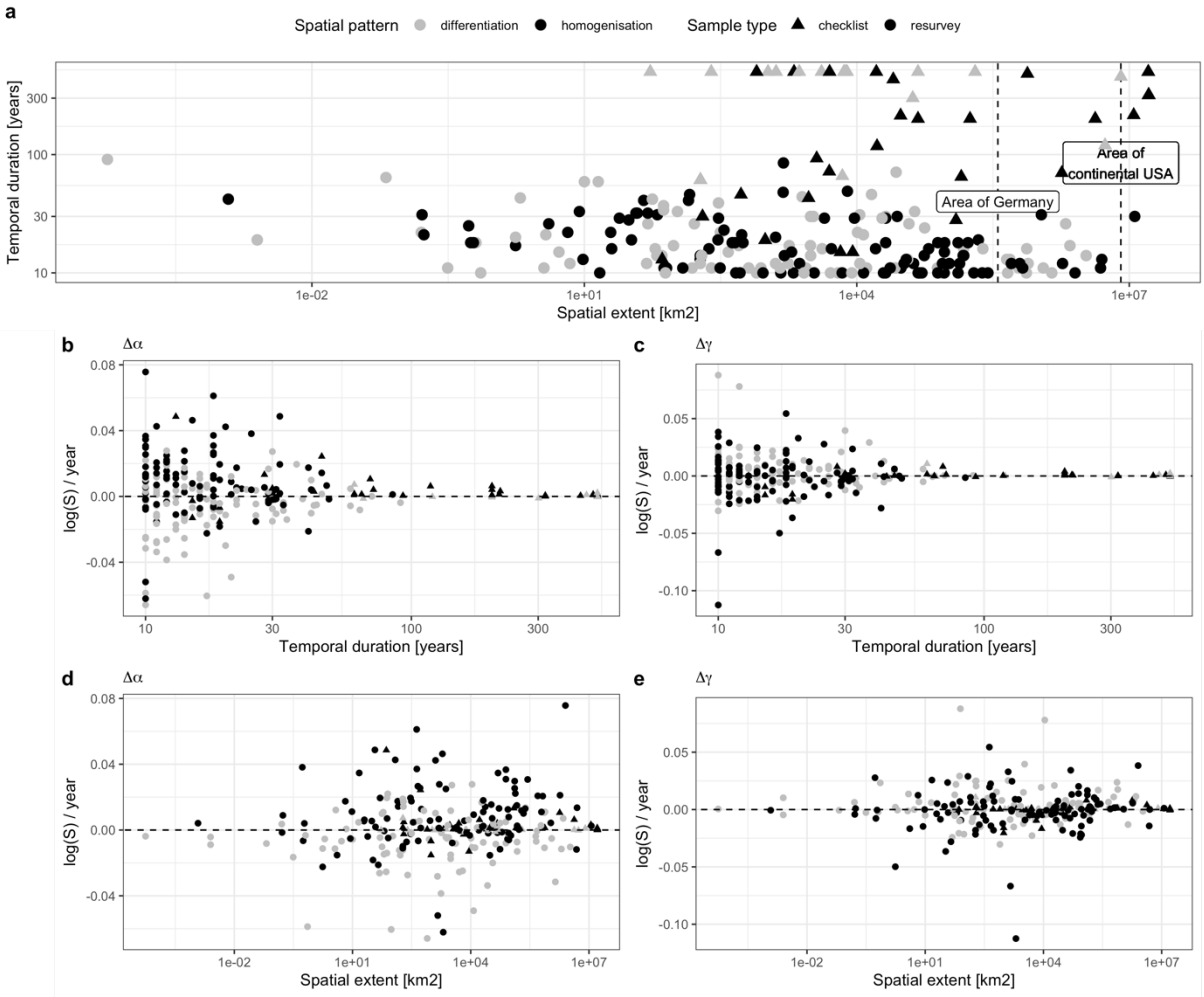
In summary, we propose moving beyond a belief in the predominance of homogenisation, and instead working to understand the variability in how spatial β-diversity changes through time, embracing the multiscale nature of biodiversity change. Specifically, our conceptual classification emphasises that different long-term studies are experiencing fundamentally different types of temporal change in spatial β-diversity (via changes in the number of species with relatively high or low occupancy). We found that homogenisation was most often characterised by gains in the number of widespread species. This suggests that there is still time to protect many rare and narrow-ranged species before they ultimately contribute to homogenisation, and that efforts to slow the spread of widespread (possibly non-native) species are vital for preventing biotic homogenisation. Furthermore, by simultaneously considering change in α-, β- and γ-diversity through time, we show how conservation practice can embrace a multiscale approach. It is increasingly recognised that many species require protection across multiple sites or at landscape (or larger) spatial scales for effective conservation[41,42]. The framework introduced here can be used to detect the occupancy changes that underpin β-diversity change, and provides links back to changes in species richness across spatial scales.



Extended Data Figure 1: Counts of locations in hexagonal grid cells (cell area = 69,968 km2). The data include 259 regions (i.e., γ-scale) and 16,359 locations (i.e., α-scale).



Extended Data Figure 2: Results were qualitatively consistent when multiple years were used to determine richness in the two periods. Parameter estimates of models fit to changes calculated using first and last year only (as per main text results) as a function of those estimated when richness was averaged over multiple years in two periods. (a) Intercept estimates for changes at each scale, (b) Realm estimates for each scale, (c) Latitudinal band estimates for each scale, (d) Sample type estimates for each scale, and (e) Taxon group estimates for each scale. Diagonal dashed line is 1:1 line in all panels; points show median of the posterior distribution, and whiskers show 90% credible interval.



Extended Data Figure 3: **Changes in β-diversity as a function temporal and spatial scales.** (a) Temporal duration and spatial extent for all datasets in our analysis; and, empirical estimates of (b) α-scale and (c) γ-scale richness change as a function of temporal duration, and (d) α-scale and (e) γ-scale richness change as a function of spatial extent. Points are coloured according to whether the empirical estimates indicated differentiation or homogenisation (i.e., above or below the 1:1 line in our conceptual figure 1); shapes denote sample type (checklist or resurvey). Dashed vertical lines on (a) show the land area of Germany and continental USA for reference. Two datasets where empirical estimates of α- and γ-scale richness change were equal to zero (and hence neither homogenising or differentiating) are not shown.

Methods

Data compilation: Our conceptual framework requires estimates of species richness changes at two scales. We refer to them as local (α) and regional (γ), the exact definition of which varies among data sources. To make our data search and synthesis as comprehensive as possible, we searched broadly for data that met these criteria, where regions had at least four plots or locations, and where richness changes were estimated over a period of at least ten years. We started by identifying 80 relevant datasets within the BioTIME database[22] that monitored patterns of species abundances within assemblages. To this, we added: (1) similar assemblage-level time series of studies not (yet) included in BioTIME (e.g., [23,24]); (2) data from studies using 'resurveys', where sites associated with a historical dataset were revisited and re-surveyed using similar methodology in more recent times; (3) data from 'checklist' studies where species known to be present in a given locality (and region) at a 'historical' point in time were indicated together with species present in that locality at a later point in time (minus those that went extinct from a site plus those that newly colonised that site); and, (4) data from studies that reported changes in species richness at two spatial scales, but for which the underlying raw data were not available. Because of the relatively specific data requirements, literature searches were conducted in an ad-hoc fashion, rather than using a formal literature search. In all, we compiled a total of 259 regions and a total of 16,359 locations that met our criteria (Extended Data Figure 1); 205 regions documented repeated samples of species assemblages through time; 54 regions were compiled from checklist studies.

Exploratory variables: In addition to differentiating sample types as either a resurvey or a checklist, we retained metadata to use in subsequent analyses that included:

- realm (freshwater, marine and terrestrial),
- geographic coordinates of all locations,
- spatial extent (km^2). Extent was calculated in two ways: most often, as the area of a convex hull (or bounding box) around all locations within a region, or for some checklist data as the sum of the area of each location within a region (e.g., sum of island areas for birds on islands distributed across the Pacific, Indian, Atlantic Oceans and the Caribbean Sea).
- the following taxon groups: mammals, herpetofauna (reptiles, amphibians), plants, birds, fish, invertebrates. For studies in BioTIME labelled as having multiple taxa, we identified the dominant taxon group (using the same groups listed above).

Data standardisation: To quantify changes in β-diversity that emerged from combined changes occurring at the local- and regional-scale, we required that the starting and end years for all locations within a given region were the same. This ensured that change estimated across the different locations within a region covered the same period of time, and meant that regional changes estimated by aggregating all species across all locations within regions also covered the same time period. Additionally, to ensure that our analyses did not quantify changes in species richness due to variation in sampling effort, we needed to standardise sampling effort (e.g., the number of plots or transects) across all locations for each time point within regions. The heterogeneous nature of the data that we compiled meant that we needed slightly different procedures to identify combinations of locations and years for different data sources. For clarity, we delineate broad categories of data structures, and describe separately how locations and years were selected and sample-effort standardised for the different structures.

Checklist data: Checklist data typically consisted of species lists for locations within regions, compiled for two time periods, historical and contemporary. These lists were compiled either from samples and/or observations collected during the two periods, or more frequently, by counting native species only to determine the richness of the historical period, with the contemporary species richness calculated as the sum of native and introduced species (minus any species that went extinct). For our analyses, we selected regions with at least four locations, removed locations that documented species lists for only one period, and finally, ensured that all locations within each region had the same year for both the historical and contemporary species lists.

Resurvey data: We distinguish three different data structures that we refer collectively to as resurvey data:

(i) data that document repeated samples of assemblages, e.g., BioTIME [22], RivFishTime[23], and InsectChange[24], and similar data that we compiled for this study. We first filtered data to ensure that samples from all locations within regions had a temporal duration of at least ten years, and that at least four locations were sampled per year. Locations within regions were identified using geographic coordinates in the data, although we also regions with only one geographic coordinate where discrete, unique samples could be identified, e.g., plots within a site.

After applying these filters, the number of locations sampled per year often varied considerably within regions, and we sought to identify locations, as well as start and end years that balanced a trade-off between the number of locations and the duration of the sampling period for each region. To do this we first identified all year-pairs -- combinations of start and end year with at least ten years separating them -- for all locations within a given region. We then determined different thresholds for what proportion of the total number of locations we wanted to retain, using a combination of the total number of locations in a region, and visual inspection of locations sampled in each year. For example, for resurvey data newly collated for this study, we selected starting and end years where the proportion of the maximum locations was at least 90% for regions with fewer than 20 locations, 50% for regions with more than 20 locations, and 25% for the NERC Countryside survey data[43–47], which had between 60 and 300 locations across the UK (and where the lower threshold meant that the duration of the region increased by more than ten years). For regions in the BioTIME and RivFishTime databases, we identified year-pairs with at least 75% and 90% of the maximum number of locations, respectively. Multiple year-pairs often remained following this, and we selected the pair of years with the longest duration, and finally, broke any remaining ties by selecting the pair of years with the most locations. For other data, specifically mosquito data sourced from Vectorbase (https://vectorbase.org/vectorbase/app), this process of selecting locations and the start and end years for each region was done visually.

Next, we ensured that sampling effort was consistent across all years and locations within regions, using sample-based rarefaction[48] where required to standardise effort. Note that for many data (e.g., InsectChange and other invertebrate data) where sampling took place across multiple months within years, we used sample-based rarefaction to resample equal numbers of samples across the same months for all locations within a region, which were then compiled to provide one sample per year for each location. Additionally, for data collected using multiple sampling methodologies (e.g., mosquitoes sampled using different attractants, or freshwater fishes collected with different

techniques), we identified the methodology that ensured the maximum number of time series, and standardised sampling effort using data collected with one methodology only.

(ii) We collated data from studies where sites associated with a historical dataset were revisited and re-surveyed using the same methodology in more recent times, sometimes referred to as "legacy" studies (e.g., [49]). Again, we required each region to have at least four locations and ten years or more between the historical and contemporary samples.

(iii) Finally, we collated studies that estimated species richness changes at two scales, where there were at least four sites at the smaller scale and ten years between the first and last sample. For these studies raw data were not available (n = 15), and we extracted an estimate of the average local richness at two time points, and a single value for regional richness at two time points.

Estimating richness and its change: For the majority of the data, we calculated species richness from the effort-standardised locations and years as the number of distinct species, though higher classifications, such as genera, were sometimes used where studies only classified organisms to genus. We calculated species richness for each location within each region for every available year to document changes in local-scale species richness. Regional-scale richness was calculated as the number of species in all sites combined for each region and each year. However, because this method of calculating regional richness yields a single number for each region at each time point, which limited our ability to fit statistical models to these data, we additionally calculated two types of resamples of regional richness: jackknife or bootstrap. Jackknife resamples were calculated by systematically leaving each location out of the regional richness calculation once, and we retained all ($n_{\text{locations}}$) resamples for our regional scale analyses. For some datasets where effort-standardisation was more complex and required the use of sample-based rarefaction, we used 200 bootstrap resamples (i.e., richness was estimated using all locations, not $n_{\text{locations}}$-1); to prevent these resampled data dominating the data to which models were fit, we subsampled the bootstrap resamples down to the same size as a jackknife would have been (i.e., we used a random subset of the bootstrap resamples equal to $n_{\text{locations}}$ for the given dataset).

Many data sources, e.g., the fifty-four regions documented by checklist data, had only two years of data available. So, to maximise the number of regions in our analysis, we calculated richness change using the log-ratio of species richness in the most recent time point and species richness in the initial sample, divided by the number of years between the two samples (i.e., $log\left(\frac{S_{t2}}{S_{t1}}\right).t^{-1}$, where S_{t2} is species richness in the most recent sample (t2 = year), S_{t1} is species richness in the first sample (t1 = year), and t = t2 – t1 + 1 is the number of years between the samples. This was done separately for each location in each region. These same data were aggregated and used to calculate concomitant changes in regional diversity through time, quantified as the log-ratio of jackknife resamples of species richness at the regional scale (i.e., the species richness of (n-1) locations within a region) in the most recent sample and jackknife resamples of species richness in the initial sample, divided by the number of years between the two samples.

Statistical models: To estimate local- and regional-scale richness changes, we fit multilevel (also called mixed effects or hierarchical) models to data from each scale separately. These models took the form:

$$ES_{ij} \sim N(\mu, \sigma),$$

$$\mu = \alpha + \alpha_i,$$

where ES_{ij} is assumed to have a Gaussian error distribution and is either the jth local-scale or jackknife regional-scale estimate of species richness change in region i, α is the overall intercept and average rate of change estimated for each scale, and α_i is the departure from the overall intercept for each region (i.e., the varying intercept for regions). Models were fit using Bayesian methods and we assumed the following, weakly regularising priors:

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

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

$$\sigma \sim N(0,1).$$

In addition to these models to estimate the overall rate of change at the local- and regional-scales, we also used models of a similar structure to examine variation between the different sample types (i.e., resurveys and checklists), realms (freshwater, marine and terrestrial), latitudinal bands (polar: |latitude| > 60º, temperate: 35º < |latitude| < 60º, subtropical: 23.5º < |latitude| < 35º, tropical: |latitude| < 23.5º), and taxon groups (birds, fish, herpetofauna, invertebrates, mammals, multiple taxa, and plants). These models replaced the single overall intercept estimated in the initial model with a parameter for each category. All models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan[50], and coded using the brms

package[51]. Models were fit with four chains and 20,000 iterations, with 10,000 used a warmup and further thinned by 10, resulting in 4000 samples of the posterior distribution. Visual inspection of the HMC chains showed excellent convergence.

To quantify changes in β-diversity ($\Delta\beta$) using these models, we combined overall estimates of changes at the local- ($\Delta\alpha$) and regional-scale ($\Delta\gamma$) as x- and y-coordinates, respectively, and calculated the distance of these points from the 1:1 line. Specifically, 1000 draws from the posterior distribution of the local-scale estimate were designated as the x-coordinate, and combined with 1000 draws from the corresponding regional-scale estimate as the y-coordinate, and the distance from the 1:1 line calculated. Accordingly, changes in β-diversity are in units of effective numbers of communities[29].

To visualise counts of the different scenarios of change, we counted the empirical effect sizes (i.e., the log-ratio standardised by duration [ES] defined above) that fell into each category; empirical estimates that fell on the border between different scenarios (e.g., when $\Delta\gamma = 0$), the count was divided between the different scenarios (i.e., we added fractions to counts when estimates fell on the border between scenarios). To visualise scale-dependence of our estimates of local- and regional-scale richness changes, we plotted the empirical effect sizes as a function of spatial and temporal extent (Extended Data Figure 2). Note that to show local-scale estimates as a single point on these figures, we used the mean of the local scale *ES* for each region.

Sensitivity analysis: To examine whether our results were sensitive to our use of two time points only in the main analyses, we repeated all analyses using multiple years to estimate the average richness for two periods where the data permitted. Specifically, for time series where more than three years were sampled, we split each time series into two halves, standardised sampling effort in each of the two periods, and calculated the average species richness in each period. Then, similar to our main analyses, we used the log-ratio of richness in the second period divided by richness in the first period, standardised by the duration of sampling in the region as our estimate of diversity changes occurring at each scale. We fit the same statistical models to these data, and our results were qualitatively consistent (Extended Data Figure 3).

References

1. Díaz, S. *et al.* Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* **366**, (2019).
2. Newbold, T. *et al.* Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS biology* **16**, e2006841 (2018).
3. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
4. Dornelas, M. *et al.* Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).
5. Blowes, S. A. *et al.* The geography of biodiversity change in marine and terrestrial assemblages. *Science* **366**, 339–345 (2019).
6. McKinney, M. L. & Lockwood, J. L. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution* **14**, 450–453 (1999).
7. Lockwood, J. L. & McKinney, M. L. *Biotic homogenization*. (Springer, 2001).
8. La Sorte, F. A. & McKinney, M. L. Compositional changes over space and time along an occurrence–abundance continuum: anthropogenic homogenisationof the North American avifauna. *Journal of Biogeography* **34**, 2159–2167 (2007).
9. Karp, D. S. *et al.* Intensive agriculture erodes β-diversity at large scales. *Ecology letters* **15**, 963–970 (2012).
10. Gossner, M. M. *et al.* Land-use intensification causes multitrophic homogenisationof grassland communities. *Nature* **540**, 266–269 (2016).
11. Socolar, J. B., Gilroy, J. J., Kunin, W. E. & Edwards, D. P. How should beta-diversity inform biodiversity conservation? *Trends Ecol Evol* **31**, 67–80 (2016).
12. Chase, J. M. *et al.* Species richness change across spatial scales. *Oikos* 1–13 (2019).

13. Whittaker, R. H. Vegetation of the Siskiyou mountains, Oregon and California. *Ecol Monogr* **30**, 279–338 (1960).
14. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of Earth's ecosystems. *Science* **277**, 494–499 (1997).
15. Barnosky, A. D. *et al.* Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
16. Vellend, M. *et al.* Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences* **110**, 19456–19459 (2013).
17. Elahi, R. *et al.* Recent trends in local-scale marine biodiversity reflect community structure and human impacts. *Current Biology* **25**, 1938–1943 (2015).
18. Primack, R. B. *et al.* Biodiversity gains? The debate on changes in local-vs global-scale species richness. *Biol Conserv* **219**, A1 (2018).
19. Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J. & McGill, B. Rapid biotic homogenisationof marine fish assemblages. *Nature communications* **6**, 1–5 (2015).
20. Martins, I. S., Dornelas, M., Vellend, M. & Thomas, C. D. A millennium of increasing ecosystem diversity until the mid-20th century. *bioRxiv* (2021).
21. Arita, H. T., Christen, J. A., Rodríguez, P. & Soberón, J. Species diversity and distribution in presence-absence matrices: mathematical relationships and biological implications. *The American Naturalist* **172**, 519–532 (2008).
22. Dornelas, M. *et al.* BioTIME: A database of biodiversity time series for the Anthropocene. *Glob Ecol Biogeogr* **27**, 760–786 (2018).
23. Comte, L. *et al.* RivFishTIME: A global database of fish time-series to study global change ecology in riverine systems. *Global Ecology and Biogeography* **30**, 38–50 (2021).
24. van Klink, R. *et al.* InsectChange: a global database of temporal changes in insect and arachnid assemblages. *Ecology* **102**, e03354 (2021).

553 25. Sax, D. F., Gaines, S. D. & Brown, J. H. Species invasions exceed extinctions on islands
554 worldwide: a comparative study of plants and birds. *The American Naturalist* **160**, 766–
555 783 (2002).
556 26. Essl, F. *et al.* Native, alien, endemic, threatened, and extinct species diversity in European
557 countries. *Biological Conservation* **164**, 90–97 (2013).
558 27. Baiser, B., Olden, J. D., Record, S., Lockwood, J. L. & McKinney, M. L. Pattern and
559 process of biotic homogenisationin the New Pangaea. *Proceedings of the Royal Society B:*
560 *Biological Sciences* **279**, 4772–4777 (2012).
561 28. Baiser, B., Valle, D., Zelazny, Z. & Burleigh, J. G. Non-random patterns of invasion and
562 extinction reduce phylogenetic diversity in island bird assemblages. *Ecography* **41**, 361–
563 374 (2018).
564 29. Jost, L. Partitioning diversity into independent alpha and beta components. *Ecology* **88**,
565 2427–2439 (2007).
566 30. Srivastava, D. S. & Kratina, P. Is dispersal limitation more prevalent in the ocean? *Oikos*
567 **122**, 298–300 (2013).
568 31. Leroy, B. *et al.* Global biogeographical regions of freshwater fish species. *Journal of*
569 *Biogeography* **46**, 2407–2419 (2019).
570 32. Rahel, F. J. Homogenisationof fish faunas across the United States. *Science* **288**, 854–856
571 (2000).
572 33. Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T. & Brosse, S.
573 Homogenisationpatterns of the world's freshwater fish faunas. *Proceedings of the*
574 *National Academy of Sciences* **108**, 18003–18008 (2011).
575 34. Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S. & Villéger, S. Worldwide
576 freshwater fish homogenisationis driven by a few widespread non-native species.
577 *Biological Invasions* **18**, 1295–1304 (2016).

578 35. Su, G. *et al.* Human impacts on global freshwater fish biodiversity. *Science* **371**, 835–838
579 (2021).
580 36. Dornelas, M. *et al.* A balance of winners and losers in the Anthropocene. *Ecol Lett* **22**,
581 847–854 (2019).
582 37. Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nature Climate*
583 *Change* **3**, 919–925 (2013).
584 38. Eriksson, B. K. & Hillebrand, H. Rapid reorganization of global biodiversity. *Science*
585 **366**, 308–309 (2019).
586 39. Diserud, O. H. & Ødegaard, F. A multiple-site similarity measure. *Biology letters* **3**, 20–
587 22 (2007).
588 40. Chao, A., Jost, L., Chiang, S. C., Jiang, Y.-H. & Chazdon, R. L. A two-stage probabilistic
589 approach to multiple-community similarity indices. *Biometrics* **64**, 1178–1186 (2008).
590 41. Boyd, C. *et al.* Spatial scale and the conservation of threatened species. *Conservation*
591 *Letters* **1**, 37–43 (2008).
592 42. Allan, J. R. *et al.* The minimum land area requiring conservation attention to safeguard
593 biodiversity. *Science* **376**, 1094–1101 (2022).
594 43. Furse, M. T. *et al.* Headwater stream invertebrate data 1990 [Countryside Survey].
595 (2016a) doi:10.5285/B4C17F35-1B50-4ED7-87D2-B63004A96CA2.
596 44. Furse, M. T. *et al.* Headwater stream macrophyte data 1998 [Countryside Survey].
597 (2016b) doi:10.5285/E0B638D5-8271-4442-97EF-CF46EA220F5D.
598 45. Dunbar, M., Murphy, J., Clarke, R., Davies, C. & Scarlett, P. Headwater stream
599 invertebrate data 2007 [Countryside Survey]. (2016a) doi:10.5285/18849325-358B-
600 4AF1-B20D-D750B1C723A3.
601 46. Dunbar, M., Murphy, J., Clarke, R., Davies, C. & Scarlett, P. Headwater stream
602 macrophyte data 2007 [Countryside Survey]. (2016b) doi:10.5285/249A90EC-238B-
603 4038-A706-6633C3690D20.

47. Wood, C. M. *et al.* Long-term vegetation monitoring in Great Britain – the Countryside Survey 1978–2007 and beyond. *Earth System Science Data* **9**, 445–459 (2017).

48. 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).

49. Becker-Scarpitta, A., Vissault, S. & Vellend, M. Four decades of plant community change along a continental gradient of warming. *Global Change Biology* **25**, 1629–1641 (2019).

50. Carpenter, B. *et al.* Stan: A probabilistic programming language. *Journal of statistical software* **76**, (2017).

51. Bürkner, P.-C. brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28 (2017).

Acknowledgements: SAB, TE, AS, RvK, WBX, JMC gratefully acknowledge the support of the German Centre of Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (funded by the German Research Foundation; FZT 118). AFE acknowledges the Fisheries Society of the British Isles Studentship.

Author contributions:

Conceptualization: SAB, BM, TE, ISM, DM, HS, NJG, AM, MD, JMC

Methodology: SAB, BM, VB, CFYC, TE, AFE, ISM, DM, FM, AS, HS, RvK, WBX, NJG, AM, MD, JMC

Investigation: SAB, BM, VB, CFYC, TE, AFE, ISM, DM, FM, AS, HS, RvK, WBX, NJG, AM, MD, JMC

Visualization: SAB, BM, TE, ISM, DM, HS, NJG, AM, MD, JMC

Writing – original draft: SAB, BM, MD, JMC

Writing – review & editing: SAB, BM, VB, CFYC, TE, AFE, ISM, DM, FM, AS, HS, RvK, WBX, NJG, AM, MD, JMC

Competing interests: The authors declare that they have no competing interests.

Data and materials availability: All data used in this study are open access. R code used for compilation (https://github.com/chase-lab/metacommunity_surveys, https://github.com/chase-

lab/checklist_change, https://github.com/chase-lab/homogenisation-richness) and all analyses (https://github.com/sablowes/WhittakerBetaChange) are available, and will be archived in Zenodo prior to publication.