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Review

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Looking back on biodiversity change: lessons for the road ahead

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Estimating biodiversity change across the planet in the context of widespread human modification is a critical challenge. Here, we review how biodiversity has changed in recent decades across scales and taxonomic groups, focusing on four diversity metrics: species richness, temporal turnover, spatial beta-diversity and abundance. At local scales, change across all metrics includes many examples of both increases and declines and tends to be centred around zero, but with higher prevalence of declining trends in beta-diversity (increasing similarity in composition across space or biotic homogenization) and abundance. The exception to this pattern is temporal turnover, with changes in species composition through time observed in most local assemblages. Less is known about change at regional scales, although several studies suggest that increases in richness are more prevalent than declines. Change at the global scale is the hardest to estimate accurately, but most studies suggest extinction rates are probably outpacing speciation rates, although both are elevated. Recognizing this variability is essential to accurately portray how biodiversity change is unfolding, and highlights how much remains unknown about the magnitude and direction of multiple biodiversity metrics at different scales. Reducing these blind spots is essential to allow appropriate management actions to be deployed.

This article is part of the theme issue 'Detecting and attributing the causes of biodiversity change: needs, gaps and solutions'.

1. Introduction

Developing fit for purpose biodiversity policy requires accurate estimates of how biodiversity has changed in the context of widespread human modification of the planet [1]. Accurate estimates of biodiversity and its rates of change is key for the development of the economic policies that fully incorporate natural capital, as advocated by Dasgupta & Levin in this issue [2]. Meeting this challenge means recognizing that biodiversity is a multi-dimensional

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concept. As we accumulate data and inference tools, it is increasingly clear that patterns of biodiversity change are complex and heterogeneous. While some biodiversity metrics are changing in synchrony at some scales, other metrics, scales, or methods show opposite trends [1]. Here, we aim to review progress towards a data-driven consensus on biodiversity change, as well as uncover where gaps remain. Specifically, we provide an overview of biodiversity change patterns from the recent literature and assess which trends are consistent in space and time, and which are not.

About a decade ago, the view of ubiquitous biodiversity declines at local scales was challenged by two independent synthetic global meta-analyses [3,4]. Both papers compiled biodiversity time series across many sites from across the planet spanning periods in the twentieth and twenty-first century. With largely non-overlapping data, both analyses found that the number of places where species richness was declining over time was approximately the same as the number of places where species richness was increasing, with effectively no observed net change in most places. Both papers also found a similar pattern with other diversity metrics (e.g. Simpson and Shannon diversity when available), leading to the conclusion that there was little evidence for systematic loss of local biodiversity within the sites and time frames examined. Such balance in gains and losses of species was previously reported. For instance, lack of evidence for systematic declines in local species richness is consistent with the suggestion by Sax & Gaines [5] that global declines in richness were not reflected at smaller spatial scales, because losses are balanced by gains of immigrant species. Moreover, evidence for stability in the number of species inspired the hypothesis that richness is under some form of regulation over time [6], and Gotelli *et al.* [7] found a consistent signal of species richness and abundance regulation across 59 assemblage time series.

Despite the consistency with some previous literature, the results of Vellend *et al.* [3] and Dornelas *et al.* [4] contradicted the widespread expectation of biodiversity loss across scales, and therefore were controversial (e.g. [8–10]). Some criticisms pointed to geographical biases and the short duration of the time-series examined [8]; others focused on the disparity between their results and the prevailing wisdom that biodiversity is declining [10]. Specifically, the finding of no net change, on average, in local-scale species richness appeared to be in conflict with: (i) projections of global-scale biodiversity trends based on assessments of extinction risk (e.g. [11]); (ii) the pervasive declines estimated from space-for-time approaches evaluating the influence of various anthropogenic drivers, such as land-use change (e.g. [12], see box 1); and (iii) the widespread disappearing populations of animals [33] and apparent declining abundances of vertebrate populations [34].

The controversy over temporal trends in local richness changes through time triggered a wave of new analyses and syntheses of biodiversity change. It has also reinforced the point that different approaches to measuring biodiversity change provide different insights into how assemblages are being restructured. Here, we provide an overview of this literature, and take stock of what has been learned in the process. We aim to identify where there is agreement in the literature and where uncertainty is highest, with the overall goal of highlighting critical gaps in our understanding of how biodiversity is changing in the Anthropocene. While we (the authors of this study) share a position in the controversy, this is not a locked-in debate (*sensu* [35]); our goal here is to synthesize the substantial scientific advances in this area. We do not underestimate the threats to biodiversity we currently face, and we share the goal of informing conservation policy by scientific evidence. We hope to build on recent efforts to pursue consensus (e.g. [10,29,36,37]), as the biodiversity change field expands beyond this single debate. We aim to identify which metrics have consistent patterns, which have divergent patterns, and where important gaps in knowledge remain. We start by highlighting the scope and methodological caveats of our review, followed by the review itself, focusing on different biodiversity dimensions across spatial scales (figures 1 and 2). We end with reflections on directions forward in this field.

2. Scope, data sources and caveats

We reviewed studies that assessed change in biodiversity in the recent decades to chart progress of understanding about biodiversity change. A systematic review and comprehensive meta-analysis is beyond the scope of this study (searches with relevant keyword combinations reveal over 20 000 publications since 2013). Instead, we aimed to synthesize compiled papers through the collective knowledge of the authors, combined with more targeted searches. We recognize the potential for bias in this approach, and attempt to minimize it by first defining what is within the remit of our study.

(i) Our study is focused on observational assessments of biodiversity change through time, rather than those predicted by theoretical, conceptual or experimental studies. The underlying data in the studies we include are observations of organisms sampled over time using consistent methods.

(ii) Our study concerns change in biodiversity through time. As such, we focused on methodologically- and effort-controlled observational time series including: groups of organisms that have been observed over multiple years, resurvey data where locations sampled in the past were resampled more recently, and regional check-lists from two or more periods at larger scales (see point (v)). An approach often used to infer biodiversity change involves space-for-time substitutions, whereby locations with different levels of a given driver (e.g. land use) are compared. This approach implicitly assumes that changes in the driver would have led to the observed changes in biodiversity had they occurred over time. We do not include space-for-time studies in the main section of our review, but in box 1, we discuss advantages and challenges of this approach, as well as how the patterns that emerge from space-for-time data compare to those that emerge from temporal data.

(iii) Our study concentrates on the recent part of the Anthropocene. We use the term Anthropocene broadly as referring roughly to the period starting in 1850, although most of the studies we include cover the past 50 years (we highlight in the text where longer timescales were examined). As with any temporal analysis, an important question concerns the use of appropriate baselines. This question has its roots in the issue of shifting baselines [98], whereby recent observations cannot capture change that occurred before observations started. In the context

Box 1. Space for time

Many different types of data have been used to infer biodiversity change in the face of anthropogenic change, each with advantages and disadvantages [13]. Here, we have emphasized temporal comparisons, which are the most direct way to estimate change over time at a given site or region. Analyses of biodiversity change from time series, however, are often criticized, primarily because (i) appropriate long-term data are often restricted in space and may not be representative of changes occurring in some types of habitats (e.g. those that are heavily modified) and in certain ecosystem types and regions of the world; (ii) changes in potential ecological drivers at a given site are not always known; and (iii) appropriate baselines are not readily known, and even some of the longest time series (including checklists) only include data from a time period after intense human impacts have already occurred [8,10,13–15]. One solution to some of these issues are analyses that can fully incorporate temporal changes and controls on external drivers (e.g. before-after-control-impact studies), but these are usually rather short-term and experimental in scope, preventing a full exposition of biodiversity change in the context of ongoing drivers (but see [16] for an example of a large data synthesis following a before-after-control-impact design).

A popular approach for estimating patterns of biodiversity change has been using space-for-time substitutions [13], where comparisons are made between sites that have received different levels of a given driver. The most comprehensive such analyses are based on the PREDICTS database [17], which have been used to estimate the influence of different levels of land-use change on biodiversity [12,18–20]. Similar synthetic datasets comparing more and less impacted sites to infer biodiversity change in the face of a given driver have been compiled, including alien species [21], habitat loss [22], nitrogen deposition [23], climate change [24], hunting [25] and grazing [26] in terrestrial systems, as well as other anthropogenic influences in marine [27] and freshwater [28] systems.

Importantly, although results are variable, these space-for-time estimates of biodiversity change point much more uniformly towards reductions in abundance, diversity and composition than has been typically observed in time series. There are several possible explanations for this difference. First, many observations of biodiversity in space-for-time analyses are taken at relatively small spatial scales and cannot necessarily be used to extrapolate outcomes at larger spatial scales, where biodiversity losses are often much more likely to be observed relative to at larger spatial scales, where both winners and losers of biodiversity change can be measured [21,29,30]. Second, human modifications are not randomly distributed on the planet, and it is possible that part of the differences detected in space-for-time estimates are independent of human modifications. Third, space-for-time analyses often compare biodiversity between the least modified environments available to sample and highly modified anthromes, such that strongly modified environments normally constitute at least 50% of the sample sites. By contrast, only 5% of monitored locations experienced a conversion of the dominant habitat type in a global analysis of the impact of forest loss on biodiversity [31]. Given that an average of about 5.3% of the land surface has experienced a change in land use per decade from 1960 to 2019 [32], the durations of studies is an important consideration: space-for-time comparisons typically over-represent change relative to the amount of ecosystem change over 50 years, whereas time series probably under-represent it. These and other explanations might account for why biodiversity time series and space-for-time substitutions often lead to different answers to the question of local biodiversity change. A priority for future research is to quantify these biases and generate combined, weighted-estimates of changes through time.

of biodiversity change, there is no obvious solution to this issue, because it is not clear what an appropriate baseline should be. One could consider a time when ecosystems had experienced minimal human influence, which would be quite difficult to identify, as human impacts are evident throughout the Holocene [99], and with megafaunal extinctions stretching back tens of thousands of years [100]. Furthermore, substantial climatic shifts have occurred over this period, making direct comparisons with current biodiversity patterns complex. Finally, the unstated assumption of a pre-human influence baseline is that nature without humans should be the goal of conservation, whereas conservation science has moved to a perspective that includes humans as part of the ecosystem [101]. Therefore, rather than representing change relative to any particular baseline, we focus on trends of biodiversity in the more recent past, a timescale of significant change in human impact on the natural world, and for which we can effectively characterize trajectories.

(iv) We include studies from across the planet, covering the terrestrial, freshwater and marine realms, and including multiple taxonomic groups. However, sampling completeness varies substantially across space, time and taxa. For example, there are considerably more data in the literature available to us for Europe and North America than for Africa or Asia. Similarly, more studies focus on vertebrates or plants than for most of the Tree of Life, and we lack information on patterns of biodiversity change for most microbes and soil microfauna [102,103].

(v) We consider four metrics identified in McGill *et al.* [104] that contain complementary information: species richness, temporal turnover in species composition, spatial differences in species composition (beta-diversity), and abundance (numerical, biomass and cover). Our unit of observation is usually an 'assemblage' (i.e. a group of co-occurring species that typically share taxonomy and/or habitats in which they live; [105]), but we also include observations of populations and ecosystem extent in the assessment of abundance trends.

(vi) Finally, to explicitly consider spatial scale, we include studies spanning local, regional and global scales. The spatial scale at which biodiversity is measured influences the magnitude and even the direction of biodiversity change [29,106,107] and is critically important for resolving the aforementioned controversy [4,5,10,104]. This scale-dependence arises because most metrics used to quantify biodiversity exhibit a nonlinear relationship with sampling effort and with spatial scale [30,108–110],

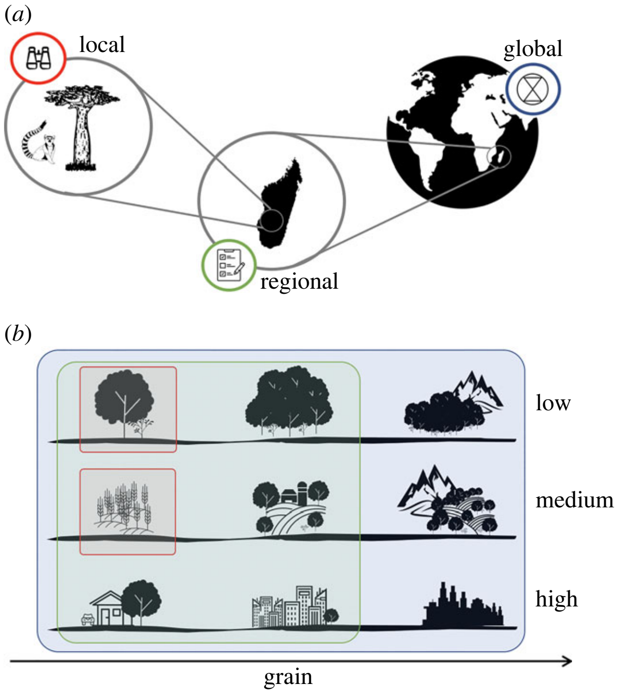

Figure 1. (*a*) Scale and methods of biodiversity monitoring. (*b*) There is a wide range of land uses (e.g. urban, agricultural) and intensity of use (high-intensity monoculture farming, parking lots and urban centres versus rangelands and rural villages) spanning through the exurbs and secondary forests (medium) to old growth forests and long-standing prairies (low). Ecologists typically sample medium to low intensity usage areas (red boxes), but large-scale studies (green box) increasingly include the whole range of land use intensities, up to the globe (blue box) which by definition includes all land uses and intensities. Thus, biodiversity trends usually sample a greater variety of ecosystem types with increasing grain size. (Online version in colour.)

caused both by statistical properties of sampling processes, as well as the ecological processes that determine how individuals of different species are distributed in space. Moreover, biodiversity is estimated using different methods (figure 1), and the temporal windows of these measurements often covary with spatial extent. For example, local scale biodiversity is typically measured via standard survey methods for a given taxon (e.g. quadrats, transects, trawls) with datasets spanning years or decades. Larger-scale regional biodiversity estimates, however, are usually derived from presence–absence data, often model-assisted, and change through time is usually estimated based on regional colonizations or extinctions; these datasets tend to span decades to centuries. Finally, many potential drivers of biodiversity change also vary nonlinearly with sampling scale. For example, when measured at a small grain, land-use intensity will be relatively uniform, whereas when measured at a larger grain, a mosaic of more and less intensive uses will combine to influence changes in biodiversity.

3. Patterns in recent biodiversity change

We organize our review in four sections, one for each of the biodiversity metrics: species richness, temporal turnover in composition, spatial differences in composition (beta-diversity), and abundance. Most of the literature we assessed does not distinguish between native and non-native species in the calculation of these metrics, focusing instead on species totals regardless of change in their ranges. Given the importance of scale-dependence, each section describes and discusses differences and similarities in patterns found at different spatial scales. Although spatial scale is a continuous variable, the same geographical distance is perceived differently by different organisms. Hence, we use a coarse classification of studies into local (from a few m to 100 km^2), regional (countries to continents) and global scales (across the entire planet). We recognize there will be some uncertainty in the classification used, but our chosen approach aligns with previous definitions of scale [30] and allows us to categorize studies in a way that balances noise and meaningful differences.

(a) Species richness

Species richness is possibly the most used biodiversity metric, but also the most controversial of the results in Vellend *et al.* [3] and Dornelas *et al.* [4]. Both of these papers found little evidence for a general trend of species richness change through time at the local scale: some sites showed increases, some showed decreases, and many showed no change. A similar pattern has been observed in several recent studies (figure 2), including on an expanded version of the original BioTIME [111] dataset with 239 additional studies (with 51 932 individual time series) from across the world [36], although not without controversy. Similar patterns emerged from several other synthetic analyses, including herbaceous plants in grasslands [112], birds [38,39], and insects and arthropods [40,113] in North America, European plants [41] and diverse taxa across marine, terrestrial and freshwater realms from 161 studies from long-term research sites in Europe [42]. However, not all analyses of species richness change find trends centred on zero. For example, species richness increases were found among coastal marine communities [43], temperate marine organisms [44], mountainous plants [45] and Canadian butterflies [46] and invertebrate communities [114]. A review of bird diversity changes found that increases in species richness was the most commonly observed pattern at local scales [47,115]. Importantly, neither increases, nor the lack of change observed on average in meta-analyses negate declines in species richness that are found in some places and/or among some taxa. For example, deep sea fish assemblages seem to be losing species locally on the whole [48], and nearly all of the above synthetic studies include declines in species richness at some locations or for some taxa. At local scales, habitat- and taxon-specific studies identify a diversity of trends in species richness consistent with the spread of richness trends detected in studies with a global extent.

At regional scales, patterns of species richness change are also mixed, but with some evidence towards more frequent increases in richness [29]. For example, numbers of species have largely increased in entire regions (e.g. spanning countries or other geographical units) for plants [49,50,107], birds [38,47] and mammals [51]. Similarly, increases in richness were found for North Atlantic fishes [52] and estuarine fishes in the Atlantic and Gulf of Mexico [53]. Likewise, Batt *et al.* [54] used changes in range sizes of marine fishes to estimate that species richness increased in eight out of nine of North American regions they studied. Yet, regional increases are not universal, with examples of

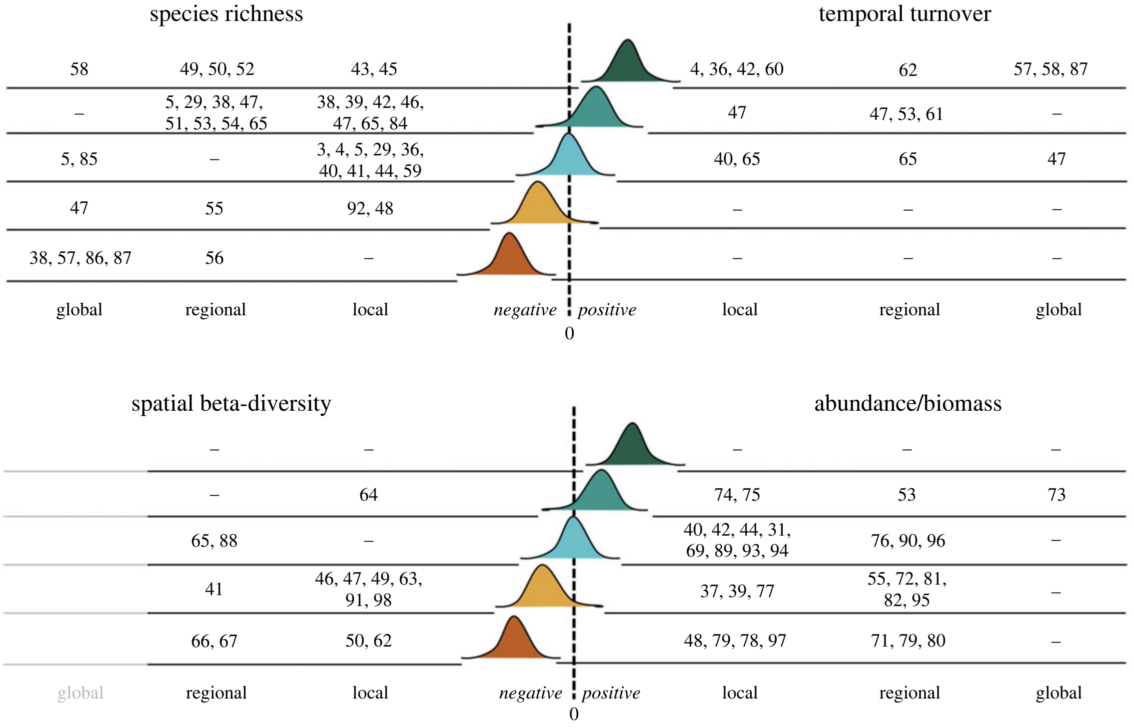

Figure 2. Classification of papers performing synthesis or meta-analysis (i.e. across many sites) in each of the 15 cells of all possible combinations of four biodiversity metrics (species richness, temporal turnover, spatial beta-diversity and abundance) and spatial scale. Rows denote a classification of the studies according to the trends reported as per the central diagram: dark green corresponds to positive trends, teal to moderate positive, turquoise to mixed trends centred on no change, yellow moderate negative and dark orange negative trends. Some studies mentioned in the text did not provide a direct estimate of a trend to be classified, and hence were not included in this figure. Figure references [3–5,29,31,36–97].

declines including bumblebees in New Hampshire [55]. Moreover, using plant occurrence data in 5 km-by-5 km grid cells from across Germany, Eichenberg *et al.* [56] observed widespread declines in species richness of vascular plants in grid cells since 1960. Using a similar approach, Bowler *et al.* [116] found increases in dragonfly richness across Germany from the 1980s to approximately 2010, followed by declines. At regional scales, richness change reversals are consistent with the hypothesis that diverse drivers of change may cause opposite trends in different locations and at different times.

At the global scale, extinction rates are high and exceed most rates observed in the fossil record [57]. On the other hand, there is also a potential acceleration in speciation rates, notably hybrid speciation in plants [58]. It seems likely, however, that the current rates of extinction exceed speciation for most taxonomic groups [117], despite such estimates being biased towards mammals and birds [118], with deficient information on temporal trends of global extinction and speciation rates for other taxa. At the global scale, despite information gaps, most studies report higher extinction rates in recent decades.

Despite being perhaps the simplest, most intuitive metric of biodiversity [119], species richness is highly sensitive to sampling effort. Consequently, meaningful comparisons can only be made when sampling effort is controlled for through rarefaction, [120], extrapolation or interpolation [121]. Importantly, even with standardized sampling effort, species richness is insensitive to some types of biodiversity change, including small magnitude changes (e.g. [122] in this issue). Hence, a robust approach to detecting biodiversity change should control for sampling effort and also avoid considering species richness in isolation.

An important motivation for quantifying change in biodiversity is to identify consequences of drivers of change (see Gonzalez *et al.* [123] in this issue for a conceptual framework to use in this context). Initial attempts to explain the range of trends observed in local species richness found that relatively little variation was accounted for by covariates. These included statistical covariates, such as the starting and ending dates, or length of the time series, as well as study-level factors such as taxonomic group, climatic region or realm (marine versus terrestrial; [4]). In Vellend *et al.* [3], even the original study authors' assessments of underlying driver variables did not account for much of the variation between studies, nor did plot area, temporal duration, or the geographical location of the studies. More recent analyses have explicitly analysed the role of potential underlying drivers of biodiversity change. For example, Suggitt *et al.* [59] found that richness increases in the data behind Vellend *et al.* [3] were associated with rapid climate change in relatively cool parts of the world, and Antao *et al.* [44] found that increases of species richness tended to be associated with warming in the temperate marine realm. Additionally, Pilotto *et al.* [42] found that increases in temperature and 'naturalness' tended to be associated with positive trends in Europe. Likewise, Daskalova *et al.* [31] showed in regions that had undergone more intense forest loss experienced greater decreases in species richness. Collectively, these studies point to complex and nuanced processes affecting species richness trends in often counterintuitive ways. Consequently, a picture begins to emerge that helps to resolve the discrepant trends found at different locations and different scales. However, there is still substantial variation in trends that is not readily predicted by specific drivers. Crucially, multiple drivers of change are affecting each location on the planet, often in different combinations [124]. These drivers can have opposing effects on species richness trends [125], and different combinations of drivers may be associated with different temporal lags, making the attribution of richness change to drivers difficult.

(b) Temporal turnover in composition

Temporal turnover (sometimes called temporal beta-diversity) [126] measures the extent of compositional change in assemblages through time, and describes a type of biodiversity change that is ubiquitous. It takes into account colonization (and/or origination) and extirpation (and/or extinction), and may additionally consider changes in the relative abundances of species. In contrast to richness, turnover metrics keep track of whether the identities of species change through time. As all assemblages undergo temporal turnover, the composition may tend to become more dissimilar from an earlier state as time goes on [127]. Hence, it is important to evaluate rates of change in turnover time series, expressed as change relative to the start of the time series (e.g. as temporal decay in similarity), rather than just comparing composition between two time points [128].

While temporal turnover has received less attention in the literature than temporal alpha (local) or gamma (global) diversity [129], it has become increasingly clear that changes in local assemblages' composition is one of the strongest signals of biodiversity change in the Anthropocene (figure 2). The first global assessment of the prevalence of these patterns [4] reported a clear signal of cumulative change in composition and elevated rates of turnover (relative to null model predictions), but this finding received less attention than the patterns found for species richness, despite the importance of species composition for the structure and functioning of assemblages and ecosystems. Subsequent work including Blowes *et al.* [36], using thousands of time series, and controlling for variation in spatial extent between studies, confirmed high rates of temporal turnover within local assemblages, that were generally higher in marine systems compared to terrestrial ones [36]. Increasingly high levels of turnover were also documented by a growing number of studies, including in plants [60,112], birds [47] and multiple taxa in Europe [42]. In some groups, like fishes [130] and ants [131], turnover leads to novel communities. Importantly, there is growing evidence the rates of local extirpation and colonization are accelerating [132]. As with richness changes, these studies reveal considerable local variation, with some communities showing limited compositional change and others showing major changes in species identities and relative abundances (e.g. [133–135]).

Although local trends in compositional change can influence turnover at regional and global scales, our understanding of rates of turnover at these larger scales is sparser. Because local temporal trends are spatially heterogeneous (e.g. [133–135]) and influenced by a number of drivers [136], it is difficult to predict how local compositional change scales up. For example, a study of ground beetles in Germany found evidence that local scale change did not lead to regional scale compositional and functional change [137]. Importantly, temporal turnover is a necessary but not sufficient condition for changes in spatial beta-diversity, as either biotic homogenization or differentiation could emerge at larger scales (see further discussion in the next section). At the global level, temporal turnover is probably increasing because of elevated extinction and speciation rates (see §3a).

There is considerable interest in the processes shaping temporal turnover across all scales. Targeted studies have found evidence that rank shifts (e.g. [138], dominance e.g. [139] and rarity e.g. [140]) contribute to compositional change, but that no single pattern prevails across all systems. Importantly, turnover is expected from natural colonization/extinction dynamics and ecological drift in the absence of anthropogenic drivers, hence it is important to know if turnover exceeds null expectations. What should or should not be included in null models that generate such expectations is in itself a topic that deserves more attention. Recent analyses showed that a small fraction of species in an assemblage contribute disproportionately to turnover [141]. Temporal turnover can be higher for non-native species than native ones [142], but the patterns are complex. In fact, turnover rates can fluctuate through time in sync with multiple environmental factors, as observed in Finnish lake plants [143] and North American desert rodents [140]. Anthropogenic activities often serve as catalysts for change, leading to increased temporal turnover, for example in the context of forest conversion to anthropogenic ecosystems [31], or following human colonization of oceanic islands [61]. There is scope for further studies of what variables drive temporal turnover across spatial scales.

(c) Spatial beta-diversity

Spatial beta-diversity quantifies differences in species composition across sites [144] or scales [145]. Here, we focus on two types of spatial beta-diversity and how they have changed through time: beta-diversity among localities within a region (local scale beta-diversity), and beta-diversity among regions within continents or over the entire globe (regional scale beta-diversity). Defined this way, there is no such thing as global beta-diversity (we do not have several planets to compare), while studies assessing beta-diversity of local communities at the global extent are rare. As mentioned at the start of §3, the classification into spatial scales is coarse, and based on our assessment of how the grain of sampling relates to organismal perception of spatial scale (i.e. a combination of dispersal potential and body size). Declines in spatial beta-diversity over time is often referred to as biotic homogenization, while increases in spatial beta-diversity over time is often referred to as differentiation [136]. Here, we assess the prevalence of homogenization and differentiation through time at local and regional scales.

At local scales, the replacement of many local endemics and specialists with a small number of wide-ranging generalist species is hypothesized to homogenize assemblages [146] for example in urban landscapes in comparison to more natural vegetation [147]. There are many studies assessing this pattern in space-for-time approach (reviewed in [148]) which we will not further discuss in this section. While there is some evidence for large ranged species replacing small-ranged ones (e.g. [41]) this does not provide direct evidence of homogenization. Among studies of how beta-diversity has changed through time, there are consistent signs of homogenization for marine fishes in Scotland [62], freshwater macroinvertebrates in New Zealand [63], Canadian butterflies [46] and birds [47]. Yet, not all studies show homogenization. For instance, marine fishes in the North

Sea have seen increasing taxonomic differentiation [64]. In fact, the largest meta-analysis of trends in spatial beta-diversity to date reveals a mix of both patterns, but a central tendency leaning slightly more towards homogenization than differentiation that was nevertheless not statistically distinguishable from no change [149].

At the regional scale, there are empirical examples across the whole range from differentiation to homogenization. For example, there was no evidence of change in beta-diversity among lake diatom assemblages of North America [65]. Comparing plant composition in historical and modern times reveals signs of homogenization among Danish vegetation assemblages [50], across Europe [49], North America [150] and globally [151]. On oceanic islands, which are strongly affected by dispersal limitation, the tendency is for homogenization driven by human introductions, although the pace and trajectory vary substantially across taxa [66]. Similarly, an analysis of biogeographic boundaries of terrestrial gastropods found evidence for regional homogenization as human introductions overcome dispersal barriers [67]. Yet, the balance between homogenization and differentiation becomes more obvious when comparing different regions across continents or the globe, where patterns in beta-diversity are tightly linked to ecosystem changes and landscape structure. Humans have modified the planet extensively, creating a patchwork of anthromes superimposed on existing biomes [99], which can generate scale-dependent ecosystem richness and diversity patterns [68]. The fragmentation (e.g. of 'original') and intermingling (e.g. with human-modified) of ecosystems is likely to impact regional beta-diversity in complex ways [152]. Considering biotic similarities of ecosystems along with changes in land use suggests there has been an increase of regional beta-diversity in the past millennium, although at a slower pace in the past century [68]. Indeed, using Whittaker's definition of beta-diversity (the ratio of regional : local richness), and following from §3a, we would expect a mixture of increases and decreases in beta-diversity to arise from the trends in local and regional species richness. In summary, these studies collectively include temporal shifts in spatial beta-diversity ranging from homogenization to differentiation, for different locations, regions and taxa.

The processes involved in mediating changes in beta-diversity are largely linked to change in patterns of connectivity and of environmental heterogeneity [153]. Human activities have been linked to homogenization patterns, through widespread introductions of species [154–156]. For example, widespread spatial homogenization of plant communities has been documented at the regional scale, primarily explained by non-native species naturalizations [154]. Conversion of natural and semi-natural ecosystems to more anthropogenic ecosystems has probably led to reduced connectivity and increased habitat heterogeneity of the remnant (semi)natural habitats (in contrast to high levels of soil and propagule transport within some human-modified ecosystems); we thus expect increased differentiation between intact and modified landscapes. Importantly, patterns of change are likely to differ considerably depending on whether beta-diversity is estimated within or across habitat types.

(d) Abundance and biomass

Abundance and biomass can also be sensitive to human impacts, and can strongly influence responses of biodiversity to global change (e.g. via sampling effects associated with the fact that observations are always incomplete samples of reality [120]). These measures differ, however, from the alpha and beta-diversity metrics discussed in the previous sections because density (number of individuals or biomass per area) can be effectively averaged across spatial subunits. That is, the change in density for a larger unit is mathematically the average (weighted by the initial value) of the changes in abundance density of each subunit. Thus, although processes controlling numerical abundance and biomass (two metrics of organismal abundance) probably do change at different scales, the patterns themselves should be mostly equivalent. Accordingly, we do not make a strong distinction of the spatial scale of analysis in this section, and instead organize the discussion by taxon. Analysis of long-term monitoring data of assemblages across diverse taxa globally reveal heterogeneity in trends in total community abundance, with the mean trend not differing from zero [4]. Other taxonomically broad surveys of communities have mostly echoed this result [31,42,69].

Results do vary among taxa, however, with more extreme rates of change commonly associated with relatively narrow taxonomic or functional groups. For example, large predatory marine fishes [157] and shark and ray [70] abundances have declined precipitously (80% and 71%, respectively). These studies focus specifically on taxa directly impacted by industrial fishing, while other studies looking at marine fishes across entire assemblages do not show these strong declines [4,44,53,132]. Indeed, Myers & Worm [157] explicitly note that compensatory responses of smaller fish species have been observed even though they were not part of their analysis. Per cent cover (a metric of biomass) of living coral on reefs has also shown large declines globally [71], while diatom abundances show spatially variable trends related to climate, without a strong overall general trend [158,159].

Terrestrial plants are estimated to have had their total global biomass reduced, as much of primary productivity is appropriated by humans, but trends are also spatially and temporally variable. Hansen *et al.* [72] found 2.3 million km^2 of loss versus 0.8 million km^2 of gain in forest cover globally between 2000 and 2012, with considerable spatial variation. By contrast, a more recent study looking at all vegetation types spanning 1982–2016 found that loss of tree cover in the tropics was outweighed by gains in temperate regions, yielding a net gain in tree cover of 2.24 million km^2, albeit with significant regional variation in both patterns and drivers [73]. Surveys of Arctic tundra vegetation found significant heterogeneity in abundance trends, with a majority of sites and groups showing no significant change overall, although five of six functional groups, particularly shrubs, grasses and sedges, showed greater increases in numerical abundance or cover than declines [74,75,160]. In the marine realm, declines outnumber and outpace increases among seagrasses [161] and kelp [162].

Trends in insect abundances have been of intense interest in recent years. A study on two forest plots in Puerto Rico [163], and two studies from multiple sampling sites and regions in Germany [164,165] reported steep declines, resulting in newspaper headlines about an 'Insect Apocalypse'. Aspects of these studies were criticized, including analysing short time series without accounting for year effects and the starting year of those time series [165–167]. Other more recent studies include a study of butterflies in Europe [76] that found that abundance declined by 50% in the UK and in the Netherlands, with 20 species declining and nine increasing in the former, and 25 species declining and 16 increasing in the latter. Similarly, in Ohio (USA) a 33% reduction in butterfly abundances was reported over 21 years [168]. Other studies have found less dramatic results. For example, a large meta-analysis of long-term sites in the USA [40] found no overall trend in insect abundance or biomass (a result that held up in reanalyses [113] after criticism [169,170]), while Daskalova *et al.* [171] found similar results in a synthetic analyses of invertebrate abundances across datasets. In a meta-analysis of time-series across the world, van Klink *et al.* [77] found distinct differences in insect abundance trends among realms, with terrestrial insects declining in abundance by 9% per decade, while freshwater insects were increasing by 11% per decade.

Studies of changes in populations of terrestrial vertebrates (typically monitored as populations rather than assemblages) have also been contentious. The Living Planet Index (LPI) monitors vertebrate populations across the world, with its most recent 2022 report showing a 69% average decline in the geometric mean of population abundances since 1970 [78]. Other studies using the Living Planet database, which is behind the LPI, have found more complex and nuanced patterns. For instance, Leung *et al.* [69] found that birds, reptiles and mammals were increasing in abundance, freshwater fishes showed no net change, and only amphibians were declining. Daskalova [172] found that 18% of vertebrate populations increased, 15% declined, and 67% showed no net change. How can these studies, using the same database, come to such different conclusions to those published in the LPI reports? A key difference is the LPI goal of averaging across all species using a geometric average and differentially weighting data series in an attempt to correct for sampling bias. Random fluctuations were found to lead to a declining LPI even when overall population trends were stable [173]. By contrast, Leung *et al.* [69] found a balance of increases and declines, once time series with fewer than six time points were excluded to improve reliability of trend estimates. Similarly, Daskalova *et al.* [172] also found a balance of increases and declines using arithmetic averages of slopes of rates of change over time. Leung *et al.* [37] further showed that the geometric average strongly emphasizes extreme changes and found that 1% of the populations showed extreme declines, 0.4% showed extreme increases and the remaining 98.6% of the populations showed no mean trend, although some regions and taxa were increasing while others were decreasing. Further, most of the extreme declines were also the shortest time series. Commentary on this analysis pointed out that there are more extreme declines than extreme increases [174], that many declines occurred prior to the 1970 baseline used by this database [175], and that the Living Planet database (and the LPI) cannot estimate change in absolute abundances [176], but is nevertheless useful for analyses of trends (i.e. are populations generally growing or declining, [177]). Other analyses that have looked at trends in vertebrate abundances with different data sources also found no overall directional trends in total abundance [4,42,132].

Among the most frequently monitored populations are birds in Europe and North America, where parallel results of a net decline in total abundance of 20% and 29% have been reported, respectively [39,79,80]. In addition, all three papers report that rare species are increasing and common species are declining. Because abundances are highly unevenly distributed among species (with 10% or fewer of the species often accounting for 50% or more of the abundance or biomass [178]), total abundance and biomass trends essentially track what is happening to the most common species. For instance, the 10 species declining the most in North America are among the most abundant [80]. Assessing human impacts on vertebrates over time scales of millennia rather than decades, Bar-on *et al.* [179] estimated that the current biomass of humans and our livestock substantially outweigh wild mammal biomass today and in pre-human times. Similarly, domesticated poultry outweigh wild birds, while marine mammals have been reduced fivefold and fishes by approximately 12%.

In summary, we are not close to a globally consistent answer to the question about total change in abundance or biomass for large taxonomic groups like insects, birds or fishes. Many of the terrestrial datasets mentioned above probably do not sample the regions with dramatic declines (e.g. intensively built or agricultural areas), which would limit their use to estimate global averages, but would instead make them representative of biodiversity trends for the very large areas outside of urban and high-intensity agricultural areas (figure 1*b*). Nonetheless, the literature shows us that for many taxa at many locations, we observe high variability centred around mean trends in biomass or abundance that are not drastically different from zero. There are more studies reporting declines than increases, and declining groups are usually either targeted for substantial harvesting, like trees and large predatory fishes, or are known to be sensitive to major global change drivers (e.g. climate change for amphibians and corals, pesticides for some birds and insects). There are also important cases where abundances seem to be increasing, possibly as a result of improved conditions, such as freshwater insects in some parts of Europe and North America [77]. Careful thinking about spatial, temporal, and taxonomic averaging (see next section), as well as averaging across functional groups (cf. [39,81]) will improve our understanding of abundance and biomass trends in the Anthropocene.

4. Steps going forward

Controversies are useful in stimulating research. However, it is useful to determine when they have been resolved, and to identify what knowledge gaps remain. Importantly, an integral component of resolving controversies is identifying where differences of opinion hinge on methodological approaches [180]. It is clear that different estimates of temporal change in biodiversity include differences that are both methodological and ‘real’. For example, in estimates of change in abundance, some studies focus on total abundance or biomass estimates for the entire assemblage (e.g. [77]), others represent agglomerated measures of population changes (e.g. [37]), while yet others represent averages across species within specified regions (e.g. LPI). Within the studies that focus on averages, the choice of arithmetic or geometric means changes the overall pattern. Geometric means of growth rates (e.g. LPI) have been shown to exaggerate extreme (and often the shortest) time series. Likewise, vote counting (per cent of species increasing and decreasing) can give very different results than estimating trends in total abundance or biomass because the most abundant species contribute more strongly to the latter and tend to dominate the overall pattern. Thus, it is important to choose methods of averaging across taxa that are appropriate for the goals and questions and to avoid direct comparisons among disparate methods.

Estimating trends that are representative of the entire planet, or any large region of the planet, will usually require combining multiple sources of data. In doing so, it is critical to consider the statistical power of contributing datasets, and to apply analytical approaches that carefully consider the underlying uncertainty and allow it to propagate appropriately. In this context appropriate meta-analytical methods should be used, either through the independent calculation of metrics of interest from sampling effort standardized raw data (e.g. [4,36]), or through the use of two-stage models (e.g. [44]). In addition, most studies also include some kind of spatial averaging. However, as a hypothetical example, a 50% decline overall could result from a 50% decline in each sub-region, a 100% decline in half the sub-regions and a 0% decline in the other half, or even a 100% decline in two thirds of the sub-regions and a 200% increase in one third of the sub-regions. Differentiating which of these scenarios are occurring is important because their implications for conservation and ecosystem function are quite different. Nevertheless, individual sites, entire regions and taxa show genuinely different and potentially opposing trends in species richness, spatial beta-diversity, abundance and/or biomass.

As data and studies have accumulated, they have revealed there is extensive variability in biodiversity trends, and that we see gains and losses of species and individuals that result in a balance of net decreases in some situations, and increases in others (figure 2). Recognizing this variation allows us to seek the underlying explanations for different patterns of biodiversity change. For instance, the rate and direction of changes vary spatially and between realms [36,42], as well as with the magnitude of different anthropogenic drivers, such as climate and land-use change [31,59,82,181]. However, much remains to be understood, as most of the variation in biodiversity trends still remains unexplained, with the added challenge that drivers of change co-occur in different combinations [124,182], making attribution a difficult task.

Many studies confirm that there is a consistent signal of compositional change over time. While some turnover is to be expected even in the absence of strong environmental change [127], there are signs that turnover is accelerating [132]. Importantly, it is likely that composition changes are associated with functional and phylogenetic changes, which do not necessarily follow taxonomic diversity trends. For example, North Sea fish communities diverged in taxonomic composition over time but converged in species traits [64]. For birds, taxonomic, functional and phylogenetic diversity increased over time in North America [39,183] while Leroy *et al.* [47] reported a balance of increases and declines in functional diversity at local scales, but increasing trends at a regional scale, and a decline globally. Climate change and fishing pressure led to opposing effects on the functional diversity of commercial fish communities in the China Seas [184]. Local, but not regional, phylogenetic diversity declined over a 19-year time series of grassland vegetation in California [185], while plant communities have become homogenized both taxonomically and phylogenetically in Europe [49] and across the globe [151]. Thus, it remains challenging to accurately predict the winners and losers of the ongoing environmental changes.

Important gaps remain in our knowledge of other facets of biodiversity, like genetic diversity, which remain largely unexplored, particularly at larger scales [186]. One of the few broad scope analyses revealed similar patterns to species richness, with generally weak or non-significant (and scale-dependent) effects of land use and human density on the intraspecific genetic diversity of greater than 17 000 species of birds, fishes, insects and mammals [187]. Other studies, however, have estimated losses of varying magnitude. For instance, a approximately 6% loss in genetic diversity since the industrial revolution was estimated for 91 species, being most severe for island species (average decline of 28%) [188], while a global loss of greater than 10% of genetic diversity was recently suggested from extrapolations of a subset of species responding to habitat loss [189]. Conversely, an increase in genetic variation following invasion was detected in both exotic and native populations for several species [190].

The evidence for a signal of biodiversity change, but not necessarily widespread loss for most measures at most spatial scales, highlights the difference between the quantity of biodiversity in a given place, and the value that particular individuals and societies assign to particular species and particular ecosystem configurations. More biodiversity, or a particular type of species or community, may or may not be desirable given a particular set of values. For example, in the management of global rangelands for improved grazing, removal of woody species can have trade-offs including detrimental impacts on biodiversity [191]. However, it is important to note that stakeholders' values are not typically determined by scientific findings, but rather by economic and societal factors related to livelihoods or highly personal moral, ethical, philosophical and political judgements. There may be important gaps between what different groups of people value, as well as between what most people value and what maximizes ecosystem function and resilience [192].

Despite the accumulation of data and proliferation of studies, important blind spots about how biodiversity is changing through space and time remain. The data available to measure change in biodiversity is consistently biased spatially, taxonomically, and with regard to anthropogenic drivers of change [193,194]. Given the variation uncovered by spatial analysis of biodiversity time series (e.g. [36,42]), as well as across taxa in the same locations (e.g. [133,195]) it is important to note that all conclusions to date are contingent on the availability of data in time, space and across taxa. We emphasize the need for improved representation of under-sampled regions and taxonomic groups. At the same time, large volumes of data are available today and we contend that these are sufficient to draw firm conclusions in relation to locations and taxa for which data are available. As we seek to expand the data to quantify these patterns, we should strive to improve representation, rather than expand to collect more of the same data. The largest ecosystem on the planet, the deep sea, remains grossly under-represented in biodiversity databases, and polar and tropical regions are also poorly covered. The most disturbed and the most pristine locations are under-represented from biodiversity databases on change through time, at a global scale [194]. Moreover, combining datasets collected with different methods continues to create important challenges to detect and attribute biodiversity change. Ideally, we would be implementing stratified random sampling of biodiversity using standardized methods across the entire planet [196,197]. Importantly, even if we start today, it will take a substantial period for time series to accumulate. Like the saying about the best time to plant a tree, the best time to begin stratified monitoring has already passed. The second best time to start is now.

5. Conclusion

There is substantial variability in biodiversity trends across metrics, scales, taxa and regions. A simplistic narrative of ubiquitous biodiversity loss does not reflect the current knowledge of empirical patterns. Recognizing this variability is imperative. Across space, time and taxa, increases and declines in a single metric of biodiversity can occur simultaneously, and different components of biodiversity may show decoupled trends. Importantly, this variability implies that our knowledge gaps matter because biodiversity monitoring is biased and there are many blind spots. Although we argue for the importance of recognizing nuance in biodiversity patterns, it is easy to fall into the trap of ubiquitous context dependence, preventing us from identifying general patterns. Instead, we argue for taking advantage of the variability in trends to help us determine what is happening in places and at times where biodiversity is changing towards outcomes aligned with our values, and where it is not. The next stage of biodiversity synthesis, that has already begun [e.g. [31,44]), will need to bring together different perspectives and quantitative analyses to improve our understanding of not only the rates and magnitudes of biodiversity change, but to quantitatively attribute those changes to drivers across the Anthropocene across scales. Identifying the types of human actions that promote preferred biodiversity trajectories will equip us to make informed decisions in biodiversity policy.

Data accessibility. This article has no additional data.

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