Review

CellPress

Fifteen forms of biodiversity trend in the Anthropocene

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Humans are transforming the biosphere in unprecedented ways, raising the important question of how these impacts are changing biodiversity. Here we argue that our understanding of biodiversity trends in the Anthropocene, and our ability to protect the natural world, is impeded by a failure to consider different types of biodiversity measured at different spatial scales. We propose that ecologists should recognize and assess 15 distinct categories of biodiversity trend. We summarize what is known about each of these 15 categories, identify major gaps in our current knowledge, and recommend the next steps required for better understanding of trends in biodiversity.

The Anthropocene and trends in biodiversity

'How bad is the biodiversity crisis?' is a question many professional ecologists have been asked in some form by lay acquaintances. Rephrased in scientific terms, this is a question about trends in biodiversity: is biodiversity improving (going up) or worsening (going down)? Not coincidentally, governments have posed the same question and identified policy goals for trends in biodiversity. The 2002 United Nations Convention on Biological Diversity (CBD) [1] set out 'to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level'.

Most people assume that biodiversity trends must be strongly negative for a simple reason: we live in the Anthropocene. The movement to name a new geological era 'the Anthropocene' [2] is a recognition of the degree to which humans are now the dominant driver of patterns in global biogeochemistry and biodiversity. Humans have [3]: (i) modified as much as 50% of terrestrial land cover; (ii) consumed roughly 40% of the Earth's primary productivity every year; (iii) doubled the annual conversion of nitrogen from inert atmospheric sources into biologically reactive forms and mined so much phosphorous that the drainage of synthetic fertilizers into the oceans has created giant anoxic dead zones; (iv) released enough CO_2 through the burning of fossil fuels that a doubling of the atmospheric concentration is likely in the lifetime of some people alive today; (v) increased the concentrations of CO_2 and other greenhouse gases with the result that short-term increases in global temperature will overshadow normal annual- to millennial-scale variation; and (vi) hunted and fished to such a degree that dominant top predators are absent or endangered on land and sea. The cumulative impact of a population of over 7 billion humans clearly warrants the geological label of Anthropocene.

For ecologists, it is both an interesting intellectual challenge and a pressing question of sustainability, ethics, and policy to understand and predict the effects of these changes on biodiversity. Given the enormous impacts humans are having, it is conventional wisdom that the changes in biodiversity must be large and negative. According to the International Union for Conservation of Nature (IUCN) Red List of threatened and endangered species, one-quarter of mammal species, one-eighth of bird species, and over 40% of amphibian species are threatened; although much less is known about invertebrates and plants, thousands of these species are also at risk [2,4] [IUCN (2014) *The IUCN Red List of Threatened Species Version 2014.2* (http://www.iucnredlist.org)]. The Living Planet Index suggests that vertebrate populations now have 52% fewer individuals than 40 years ago [5]. There are discussions of an impending sixth major mass extinction analogous to the previous five documented mass extinctions [6,7]. The great negative impact of humans is so well accepted that many ecologists have largely moved on to exploring questions of the implications for humans of this impending decline of biodiversity [8,9].

However, if we examine the literature on empirically documented trends in biodiversity, a complex picture emerges with many contradictory results. For example, total biodiversity on many oceanic islands, often perceived as among Earth's most fragile ecosystems, has stayed steady or even increased, despite repeated waves of extinction that have accompanied the arrival of humans on islands [10]. There is considerable empirical evidence that continental biodiversity at regional or local scales is also holding steady or increasing [11]. Three recent analyses [12–14] that collectively assembled published data from hundreds of biodiversity inventory studies found that local diversity is, on average, constant. Indeed, almost all human impacts can have positive as well as negative effects on biodiversity (Box 1). Over much longer timescales, paleontological data show that life is surprisingly resilient [15,16]. Many of the most dire projections of biodiversity

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Glossary

We define these terms in the context of species-based metrics of biodiversity, but many can also be applied to genetic and ecosystem diversity. The focus is on defining the concepts rather than discussing the many metrics that currently exist to quantify them.

Types of diversity

Alpha (α) diversity: the number of species present (e.g., the number of colors in one community Figure I).

α-diversity trend: change in α diversity through time (plotting α diversity for one community over time (e.g., the four blue lines on the right of Figure I).

Spatial beta (β) diversity: change in community composition across space (e.g., comparing similarity between communities a–d for one time period). This is usually plotted as similarity versus distance (distance decay), as in the three red lines at the top of Figure I labeled β (note that communities are almost always less similar the further apart they are, but the rate of decay can differ, as is the case here for each of the three time periods).

Spatial β-diversity trend: temporal change in spatial β diversity (plots the rate of decay of similarity with distance versus time period; top red line in Figure I). One common example is when the decay constant decreases through time (i.e., spatial β diversity decreases through time), as in Figure I. This type of trend is often referred to as biotic homogenization.

Temporal β diversity or turnover: change in community composition through time, usually quantified as the similarity between each time step and the time-series baseline. Usually represented as a plot of similarity versus time of separation (the four red trend lines on the right of Figure I) and measured by the rate of decay.

Spatial scales

Biogeographical: a scale within which speciation and global extinction are dominant processes [64].

Global: the entire planet.

Local: a scale dominated by species interactions and environmental constraints.

Meta-community: a scale that includes spatial heterogeneity and within which dispersal is the dominant process.

Species classification

Extinction and colonization dynamics: the recurring process of species entering and exiting a community of interest, leading to a dynamic equilibrium [65].

Losers: species that are decreasing in their abundance, range, and/or occupancy through time, the extreme being extinctions (red lines, left and middle columns in Figure 3 in main text).

Winners: species that are increasing in their abundance, range, and/or occupancy through time, the extreme being globally invasive species (green lines, left and middle columns in Figure 3 in main text).

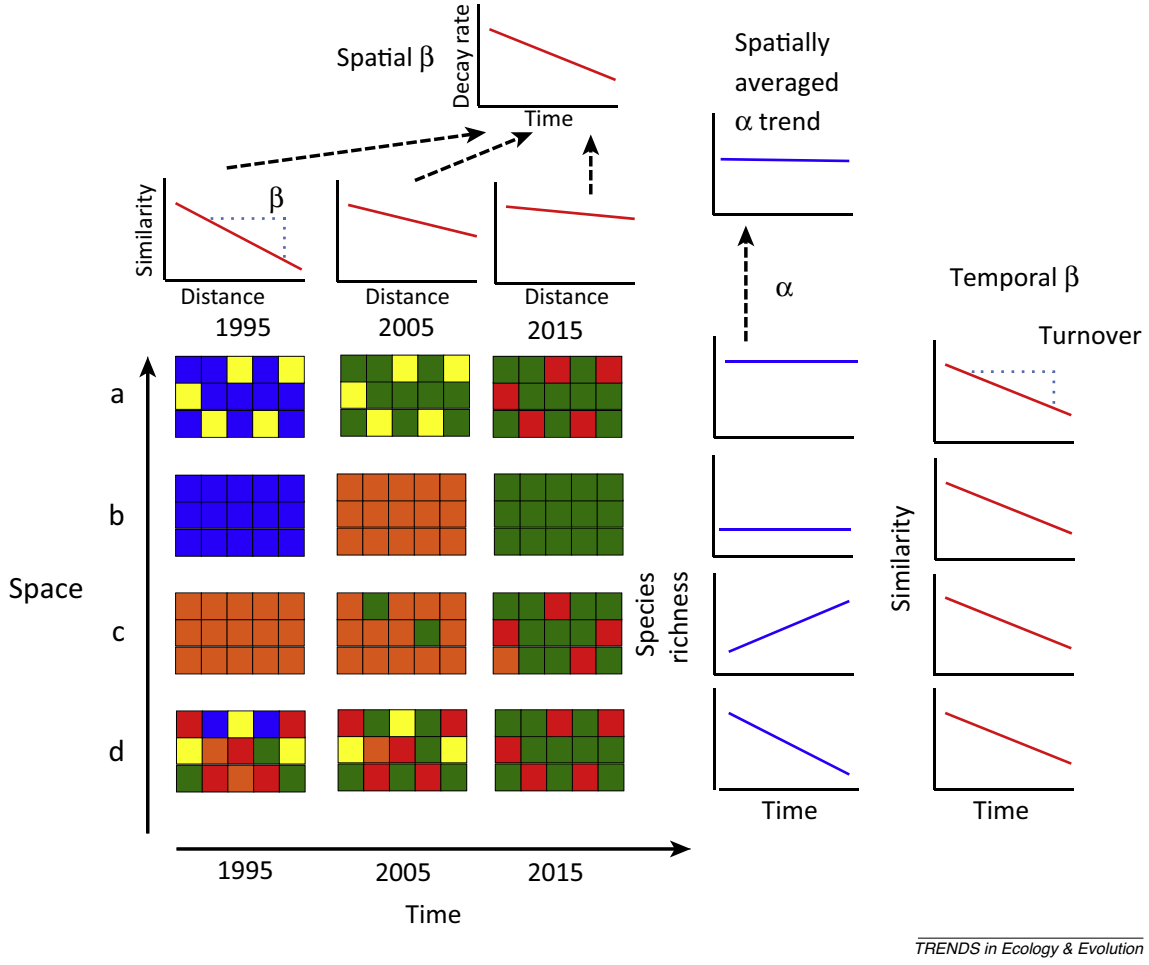


Figure I. Illustration of key types of biodiversity that can be measured. This figure follows four hypothetical communities (a–d) through three time periods (1995, 2005, 2015) (community abundance is constant, colors represent distinct species) demonstrating all of the major types of trends of α and β diversity.

loss are based on simple models of habitat change that are extrapolated to forecast future loss [6,7,17] rather than empirical observation of current trends in biodiversity and species richness. While in no way arguing that biodiversity is not in grave danger, we do argue that it is time for a measured and careful assessment of empirically quantified trends. In the following sections we suggest how best to organize this empirical assessment.

Reasons for mixed results

We suggest, as have Sax and Gaines [11] previously, that the apparently contradictory results of biodiversity-monitoring

Box 1. Types of anthropogenic impact on biodiversity

Human impacts on biodiversity are not single dimensional. Following the Millennium Ecosystem Assessment [3], we identify five broad categories of human impact with the potential for resulting biodiversity trends to differ by category. Current ecological theory is relatively weak in enabling us to predict how anthropogenic impacts will change biodiversity, so most of our knowledge to date is empirical. We summarize here the current knowledge of how five different human impacts affect biodiversity.

- Land-cover change – human-caused land-cover change typically decreases species richness in the changed area. However, by creating more heterogeneous habitat structure, meta-community to biogeographical-scale species richness can increase by, for example, bringing in edge or open habitat species (see Figure 1 in main text) [66]. Also, during restoration or recovery from disturbance, species richness often peaks at intermediate successional stages rather than either immediately after change or at the original 'climax' state [67].
- Chemical release – detrimental pollution often, but not always, decreases richness (e.g., mine tailings [68], insecticides [69], acid rain [70]). The effects of fertilizer pollution (i.e., eutrophication) are more complex, with richness both increasing and decreasing depending on various factors [71,72], although the biomass of producer and detrivore levels usually increases.
- Overharvesting – nonselective harvesting has drastically decreased biomass as well as species richness [73,74], but selective harvesting of top predators can sometimes lead to predator release with increased biomass or species richness [75]. Grazing can increase or decrease plant species richness, depending on interactions with available nutrients [76].
- Climate change – although dire predictions of species loss due to climate change have been made [17], it is difficult to prove that any modern species has gone extinct due to current climate change. The paleontological record provides a mixed record of examples, with North American trees losing only a single species [77] and North American small mammals gaining species richness due to invasions through the glacial–interglacial cycles of the Quaternary. Tree diversity in Asia shows similar patterns, whereas Europe lost a significant number of tree species during the same period [78].
- Species transport/invasions – with the exception of invasive predators on islands that had not previously experienced predation [79], it is difficult to document extinctions of species due to invasions at large spatial scales. Evidence for invasion-caused local-scale extinctions is not unheard of, but also not common [80]. However, both modern [10,11] and paleo records [15] show that large bursts of interchange increase richness at the larger scales.

Thus the effects of anthropogenic impacts on biodiversity are complex and varied. In particular, anthropogenic impacts can both increase and decrease species richness. Until we have a very good understanding of the magnitude of each of these effects in different situations, it would be difficult to tell from averaging across human impacts what the overall trend would be.

studies versus other sources of information are largely due to comparisons of apples with oranges. Specifically, we argue that achieving an accurate and general assessment of trends in biodiversity depends on the recognition of two key dimensions: the type of biodiversity measured and the spatial scale of the observations. We propose that progress in understanding biodiversity trends depends on explicitly addressing these two aspects.

Biodiversity: what is it and how do we measure it?

What do we mean when we say that a wheat field has low biodiversity compared with a tropical rainforest or that an intertidal mud flat has low biodiversity (at least of macrobes) compared with a coral reef? The most obvious difference is simply how many different species *in toto* are found there. Species richness is the most natural measure of alpha (α) diversity. However, there are other reasons why we rate the field or mudflat as low in biodiversity. Experience leads us to expect variation across space [18]; without it, we consider a system low in biodiversity. This aspect of diversity is known as beta (β) diversity [19]. Beta diversity is the change in species composition per unit space (or time; see Glossary); relatively homogeneous systems such as wheat fields and mudflats lack this spatial turnover and change in species composition. The final reason we say a mudflat (although perhaps not a fertilized wheat field) is low in biodiversity is simply the paucity of biomass (or numerical abundance of organisms). This example suggests that measures of abundance and biomass should also be considered when assessing human impacts on biodiversity. Biomass is often strongly correlated with various ecosystem functions [20] and abundance and species richness are correlated [21,22] suggesting value in disentangling the two effects.

In this review we do not consider important technical details associated with measuring the biodiversity of different taxa; nor do we address potentially informative measures of phylogenetic, functional, or trait diversity. Although species-level and ecosystem-level trends remain a core objective in conservation research, we focused here only on community-level trends (but see Box 2 for a discussion of the links between species and community trends).

Spatial scale

Spatial scale can profoundly influence the conclusions drawn about a system under study, even leading to the identification of opposite patterns and different processes at different scales [23,24]. Nonetheless, ecologists sometimes neglect spatial scale when evaluating biodiversity (also see [11]). Any link between local and global scales of, say, avian species richness must be extraordinarily weak: there are an estimated 10^{11} individual birds worldwide [25], but only approximately 1000 birds in the typical census transect. The eight orders of magnitude difference means there are 10^{7400} distinct local communities that could be sampled from the global community. Additionally, even a single extreme process (e.g., cutting down forest and creating forest fragments) can result in opposite biodiversity trends at different spatial scales (Figure 1). Although spatial scale is a continuous variable, here we recognize four distinct scales of organization for biodiversity studies: local, meta-community, biogeographical, and global.

The 15 forms of biodiversity trend

Many of the contradictory findings on trends in biodiversity result from a failure to deal with the many scales and many measures of biodiversity, each of which can vary independently. Recognizing four spatial scales (local, meta-community, biogeographical, and global) and four classes of biodiversity metrics (α diversity, spatial β diversity, temporal β diversity, and abundance) yields 15 distinct categories of biodiversity* (Figure 2). What follows is a

*There are only 15, not 16, categories because, by definition, spatial β diversity cannot be measured at the smallest (local) spatial scale.

Box 2. Stable community dynamics hide high species-level variability

The most common species-level analysis is to ask whether abundance (or occupancy) is trending up or down (i.e., distinguishing 'winners' and 'losers' [81]). The proportion of losers has been asserted to be much higher than the proportion of winners [49]. However, empirical assessments often find winners exceeding or equaling losers. There are more winners than losers in terms of abundance change in 25 years of breeding-bird data from the Netherlands [82] and in terms of occupancy among British plants [83]. North American Breeding Bird trends in abundance are about equally split between winners and losers [84], but there are more losers than winners among British butterflies and birds [83]. A careful meta-analysis on this question is clearly needed. Winner and loser species are not random, with several studies finding traits such as body size, fecundity, and resource specialization make winning or losing more likely [49,82,85,86]. The Living Planet Index (LPI) [87] attempts to aggregate individual trends in abundance to a community-level indicator. The LPI, focused only on vertebrates, has a consistently negative trend that varies with biogeographical region and taxon [65]. Alternatively, one can track changes in total community abundance (see Figure 3 in main text), which has the advantage of minimizing bias in the choice of species.

Species richness is the sum of the original richness plus all colonizations and extinctions [88–91] (other biodiversity indices are also affected but in a less linear fashion). This means that constant species richness can be compatible with significant change in species composition (i.e., a dynamic equilibrium) [88]. Dornelas *et al.* [12] found that species richness was, on average, constant, even while temporal β diversity was extremely high (10% of species colonized and another 10% went extinct each decade) (see also Box 3).

Whether looking at winners and losers, community-aggregated trends of species abundance, or colonization-and-extinction dynamics, it is important to remember that the trend of a single species is not coupled to the trend of the community it is embedded in. Even constant community trends in biodiversity can hide high variability in individual species trends, with both winners and losers and colonizations and extinctions. This argues for better quantification of turnover (temporal β diversity) as well as discussions about whether the quality of the biodiversity is changing.

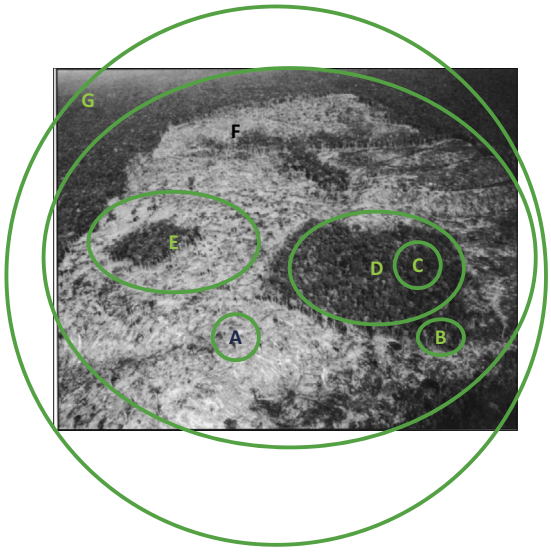
brief review of what is currently known about each of these 15 types of biodiversity trend. To help with navigation, we have given the abbreviations for each of the 15 types of biodiversity in the sections below.

Temporal trends in α diversity

α-G: Of the 15 categories, we currently know most about empirical trends in α diversity. There is good evidence that, globally, species extinction rates have increased relative to the background rate found in the fossil record by tenfold to 1000-fold [7,26], although one must be careful about the temporal scale over which rates are measured [26]. We know little about speciation rates, with arguments for both a decrease [27] and an increase [28] during the Anthropocene but no relevant empirical measurements. If we assume as a null hypothesis that speciation rates have remained constant while extinction rates have increased, global species richness should be decreasing. An estimate of 100 extinctions per million species-years (E/MSY), with the big assumption that speciation rate changes are immaterial, gives a 1% decline every 100 years. If this rate of decline were to continue exponentially for 13 800 years, this would qualify as a sixth mass extinction (i.e., >75% species lost). Even if this extreme scenario is discounted, it seems likely that global α diversity is decreasing.

α-B, α-M: Studies at the biogeographical scale are less common, but there are still enough to be reasonably confident about the overall trends. At regional scales (including islands, states, watersheds, and other areas considerably larger than traditional ecological study plots), diversity has often increased [11,29], which was presaged by analyses of biotic exchanges in the paleontological literature [15]. Increases in species richness seem strongest in plants but have also been detected in some studies of mammals, reptiles, and freshwater fish. Terrestrial bird species richness has remained relatively constant and there are too few data to draw conclusions about invertebrates. Dissection of species loss and gains in specific regions typically show nontrivial regional-scale extinctions (often attributed to human causes), but these appear to be compensated for by regional colonizations and deliberate introductions of non-native species (Box 3). There is less information about the state of regional α diversity in the marine realm, but an increasing literature on marine invasive species suggests that the patterns are consistent with those of the terrestrial realm.

α-L: Until recently, there had been little effort to assess overall trends in small-scale local (α) richness, despite the fact that this is the scale at which most ecologists work. However, this has changed with a cluster of analyses published in the past year. Vellend *et al.* [13] examined vegetation plots from 168 monitoring studies of unmanipulated systems and found that the overall trend line in species richness across studies was not significantly different from zero. Dornelas *et al.* [12] performed a similar study, assembling data from 100 high-quality monitoring studies of terrestrial plants, marine phytoplankton, birds, fish, and other taxa. They also found that, although there was great variation in richness trends between sites, the overall trend was not significantly different from zero. In contrast to the Vellend and Dornelas compilations, Supp and Ernest [14] examined studies in which experimental manipulations were performed,– ranging from exclosures and eutrophication to logging, burning, and grazing (all in terrestrial systems in which vertebrates and insects were monitored). They also found no systematic directional trends in species richness or total abundance. Murphy and Romanuk [30] analyzed a set of manipulative studies but detected statistically significant declines in biodiversity, although the use of search terms like 'species loss' and counting only native species suggest a focus on a different question than the aforementioned studies, looking primarily at single, specific human impacts on native species loss rather than overall trends in nature. Despite differing methodologies and criteria for inclusion, these meta-analyses collectively support a consistent conclusion that, for both marine and terrestrial local communities, amid large individual variation, the overall biodiversity trend is flat, with an average slope that is surprisingly close to zero. A caveat is that these studies focus on the last 50–200 years and do not exclude the possibility of a 'biodiversity cliff' several hundred years in the past. With hindsight, these results were perhaps presaged by theoretical studies of 'zero-sum' dynamics in community ecology [31,32].



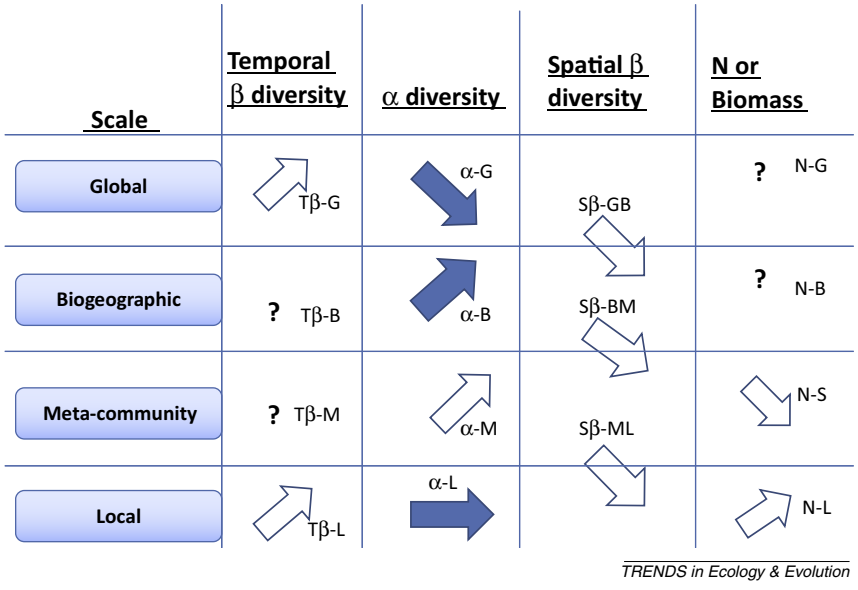
	Trend	Cause
A	↓	Habitat degradation
B	↑	New habitat
C	↓	Sink loss
D	↓↑	Sink loss, new habitat
E	↓	Habitat degradation>new habitat
F	↓	Habitat degradation>new habitat
G	↑	New habitat>sink loss

TRENDS in Ecology & Evolution

Figure 1. Complexity and scale dependence of biodiversity trends. This photograph is from the Brazil Dynamics of Forest Fragmentation Plots [92]. A previously contiguous forest was fragmented by clear-cutting. Only the remnant forest fragments were monitored, but here we combine those results with speculation about likely outcomes in the clear-cut areas and in the larger forest. Depending on the location (e.g., circles A vs B vs C or D vs E) and the spatial scale (e.g., circles C vs D vs F vs G), biodiversity may increase or decrease. The impact of deforestation on biodiversity depends on the interaction of at least three factors: (i) habitat degradation – the direct loss of species due to the conversion of forest habitat into clear-cut areas; (ii) sink loss – the loss of sink species due to the isolation of forest fragments; and (iii) new habitat – the introduction of open areas and habitat edges, which can potentially bring new species into previously forested areas. The effects of forest fragmentation are also taxon specific: in the Brazilian study, groups such as large mammals, primates, and many insects declined in species richness in the fragments whereas groups such butterflies and frogs increased (largely due to edge effects) and small mammals stayed constant [66]. Photograph copyright Oxford University Press 1992 and used with permission.

Temporal trends in turnover (temporal β diversity)

Tβ-L: There is growing evidence that temporal turnover is unexpectedly high at local scales. Dornelas *et al.* [12] quantified the temporal turnover of complete assemblages – measured relative to the baseline of the initial observation in each study – in 100 assemblages from biomes across the Earth. In over 75% of the assemblages, each of the four metrics analyzed revealed high levels of turnover (10% of species per decade) that were well in excess of the expectation of two different null models of assemblage change (also see [14]). Many individual case studies support this conclusion. For example, Rittenhouse *et al.* [33] detected marked changes in the structure of North American bird communities over



TRENDS in Ecology & Evolution

Figure 2. Schema identifying 15 distinct trends in biodiversity. By breaking out spatial scales (here treated as four discrete scales) and different aspects of biodiversity, we identify 15 different types of trend. For example, α-B is a trend in species richness [i.e., alpha (α) diversity] at the biogeographical scale and N-L is a trend in abundance (or biomass) at the local scale. There are only three spatial beta (β)-diversity trends because spatial β diversity is a comparison across two scales. Unbroken arrows indicate knowledge of trends with substantial empirical data. Hollow arrows represent commonly hypothesized trends, often based on particular anthropogenic influences (Box 1) but not measured empirically often enough for us to feel confident about them. Question marks indicate four biodiversity trends identified in this schema about which there is little empirical evidence and little speculation.

Box 3. Extinctions and colonizations on Hawaii

Although islands have provided textbook examples of the speciation and evolution of isolated populations, their biodiversity has usually been modeled in terms of contemporary ecological processes involving both natural colonizations and extinctions [88]. However, human effects are greatly increasing the rates of turnover on islands. An especially well-documented case study is Hawaii.

In the Hawaiian archipelago, there are 32 extant species of land bird, which represent the survivors of two successive extinction waves precipitated by human arrival on the islands [93]. The Polynesian settlement wave *circa* 1600 years ago decreased the avifauna from an estimated 139 prehistoric species to a historical fauna of 55 species. The second, European colonization in the 18th century reduced the numbers to the current count of 32 extant species.

The causes of extinction differed between the two waves. In the first wave, there was a pronounced loss of ground-nesting species and large-bodied species, both of which were probably the targets of selective hunting. This pattern of size-selective extinction following initial contact with humans seems to be the rule for insular avifauna [86]. In the second wave, body-size effects were not so pronounced and habitat destruction, exotic predators, and mosquito-transmitted diseases may have been more important.

However, since the arrival of Europeans approximately 55 naturalized species have been added to the Hawaiian avifauna [10]. Among different island archipelagoes, the number of introduced bird species was correlated with island area and with human population density. In terms of species richness, these 55 non-native species have more than compensated for the loss of approximately 23 species since the arrival of Europeans. Even without considering evolutionary changes, these ongoing waves of extinction and species introduction have continued to change the composition of the Hawaiian avifauna.

For plants, Sax *et al.* [10] found that the introduction of new species dominated island turnover patterns and far outweighed extinctions. In the Hawaiian islands, the estimated number of extinctions of vascular plant species has been 71, compared with 1090 species introductions, with no asymptote in sight.

These island studies suggest that long-term trends in biodiversity metrics such as species richness (see Figure 3, in main text, third column) can be profitably analyzed in terms of extinctions, colonizations, and changes in relative abundance (see Figure 3, in main text, first and second columns).

20 years, attributed to forest disturbance and forest regeneration.

Tβ-B: Turnover rates are clearly scale dependent. For example, Thuiller *et al.* [34] documented high turnover in plant community composition in the fynbos at the local scale, with 74% of sites experiencing >50% turnover between 1966 and 1996, but found no significant turnover at the regional (all-sites) scale. Ultimately, turnover is due to colonization and extinction, which may be 'natural' or anthropogenic such as human-driven homogenization [35,36].

Tβ-L: Perhaps the most extreme form of turnover is regime shifts, often attributed to climate and over-harvesting [37]. Data from various taxa, often in marine [38] or freshwater [39] systems experiencing regime shift, suggest that temporal turnover rates have increased in recent decades.

What we know about trends in spatial β diversity

Trends in spatial β diversity reveal whether the degree of similarity between sites (e.g., distance decay[40]) changes over time; homogenization [6] is when different sites become increasingly similar to each other in composition.

Sβ-L: At local scales, temporal trends in spatial β diversity are highly variable because they depend in part on change in land-use practices. For example, bottom trawling has consistently homogenized marine benthic communities [41]. Sun-coffee plantations have much lower spatial β diversity of ground-foraging beetles than shade-coffee plantations [42]. Urbanization drives homogenization of bird β diversity [43], although its effect is modulated by city size [44]. Hence, depending on historic changes in land (and sea) use, spatial β diversity in different systems has increased, decreased, or remained the same.

Sβ-M, Sβ-B: At meta-community to regional scales, there is evidence of a temporal decrease in spatial β diversity associated with increased movement of people (e.g., species transport in ballast water associated with shipping traffic [45]) and changes in land use that are similar across space [46] (e.g., increased urbanization [47]). However, this decrease in β diversity seems to be largely driven by either the introduction of exotic species (e.g., [36]) or the spread of native species [48] rather than the loss of local species.

Sβ-G: A logical extension from regional homogenization is that it leads to a globally more homogeneous planet [49]. However, to our knowledge, empirical tests at this scale are still lacking.

What we know about trends in biomass and abundance

N-L, N-M, N-B, N-G: Surprisingly, there has been relatively little work done on spatial variation in abundance or human impacts on total abundance, although the strong sampling effect of abundance on species richness and other diversity metrics is well known [12,14]; research to date has mostly shown no trend in total abundance [30].

However, there has been much research on assemblage biomass, which integrates total abundance with body size per individual [50].

N-L: At local spatial scales, enrichment of nitrogen, phosphorous, and other limiting nutrients often leads to increases in biomass in both terrestrial [51] and aquatic [52] ecosystems. However, these bottom-up effects [53] are usually accompanied by shifts in species composition [54] and trophic status [55] and are often mediated by top-down processes [56] and interactive effects of colimiting nutrients [57].

N-M, N-B: At regional or meta-community scales, total biomass may decrease because of harvesting, over-exploitation, cultivation, or changes in land use [58–60].

N-G: It is difficult to estimate the net effects of these positive and negative processes at biogeographical and global scales, although it is clear that human activity has now diverted a substantial fraction of global net primary production [61].

Uncertainty and variation in the 15 biodiversity trends

Even for well-studied topics such as trends in global α diversity, there is much uncertainty about the quantitative rates of change. Some of this variability is due to innate heterogeneity in natural systems, where underlying trends

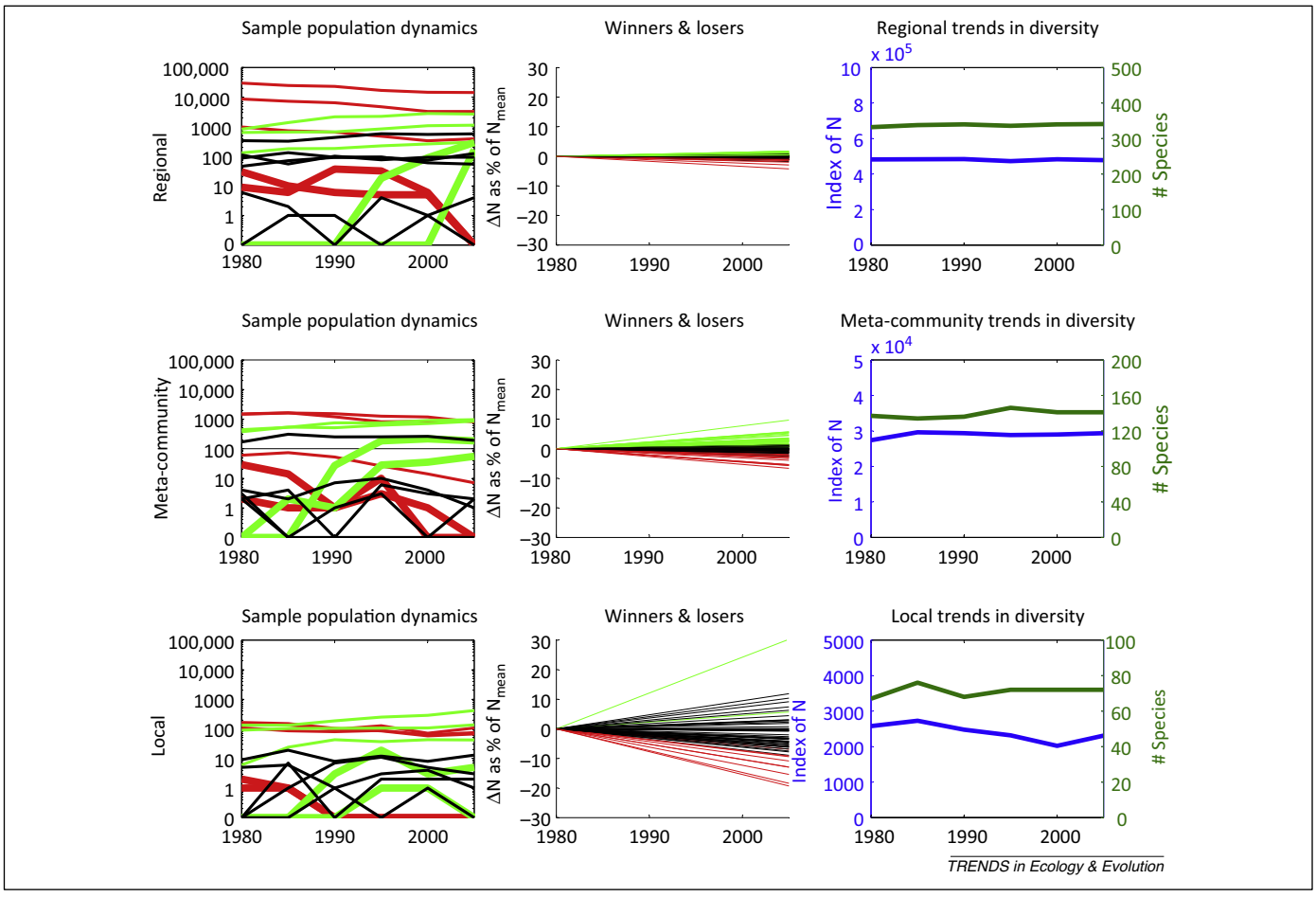


Figure 3. Variability in outcomes at the species level are common but need not create trends at the community level. Example data from the North American Breeding Bird Survey [94] (all data summed across 5-year periods centered on 1980, 1985,. . ., 2005 and for 120 routes classified as high quality). Rows show different spatial scales; the top row covers the continental USA and southern Canada; the middle row is a 5° × 5° area around Pennsylvania, USA; the bottom row is one 25-mile (~40 km) route. Note that variance increases as spatial scale decreases but overall patterns do not change. Columns show different levels of aggregation of data. Left column: Time series of a subset of individual species chosen to illustrate typical patterns. Declining species (losers) are shown in red, increasing species in green, and species without major trends in black (still showing considerable variation). Thick green lines represent species colonizers in this community and thick red lines represent species that experienced local extinction (none of which went globally extinct). Many of the black lines also show intermittent local extinction and colonization dynamics (each point is the average for 5 years, so year-level data would show even more variation). Middle column: Linear trend lines in abundance using the same data (small populations removed for clarity). Populations with statistically significant upward trends are shown in green, statistically significant downward trends are in red, and not statistically significantly different from zero is shown in black. Right column: Trends in community patterns (total abundance observed in blue and species richness in black) are much flatter than trend lines for individual species.

vary among taxa, regions of the globe, relative balance of different anthropogenic influences, and time period measured. However, much of the variability is uncertainty due to the difficulty of measuring biodiversity at multiple spatial scales. For example, as mentioned above, uncertainty about increases in Anthropocene global extinction rates over background rates varies by orders of magnitude, largely because of uncertainty about current extinction rates: the IUCN lists fewer than 850 documented extinctions [IUCN (2014) *The IUCN Red List of Threatened Species Version 2014.2* (http://www.iucnredlist.org)] over 500 years (i.e., less than two extinctions/year), but others have imputed extinction rates as high as 100 000 species/year [62] – and this is one of our best-studied biodiversity trends. Because both the natural variability and the uncertainty of our measurements are so high, reporting means for the 15 biodiversity trends without providing estimates of variability or error bars would be misleading. It is also important to note that even flat (zero-slope) trends in community biodiversity can mask enormous variation in species-level patterns, to the extent that communities trending upward can still contain many species trending downward and vice versa (Figure 3 and Boxes 2 and 3).

Concluding remarks: what we do not know and the necessity of focusing on quality in addition to quantity in biodiversity assessment

We have argued that confusion around biodiversity trends arises when discussions ignore spatial scale and types of biodiversity and thereby compare apples with oranges. Our review has identified 15 different categories of biodiversity trend. We hope that this approach can bring clarity to the measurement and assessment of biodiversity trends in the same way that Rabinowitz's seminal paper on seven forms of rarity [63] brought clarity of language and improved approaches to measuring rarity in the conservation world in the 1980s.

Probably the most striking fact from an examination of Figure 2 and the corresponding literature is how little we know (Box 4). Even patterns that seem well established, like the global decline in biodiversity (α-G), have never been directly measured and rely on models to estimate the

Box 4. Outstanding questions

Improved data

More data collected

To address 15 different types of biodiversity trend across the whole planet and all taxa requires enormous amounts of long-term time-series data, something that is lacking at present. Several approaches to obtaining this data are available.

- Include relevant data in publications – greater availability data already collected and published through electronic supplements and online repositories would substantially improve understanding of biodiversity change; reporting primary observations rather than summary indices, and including abundances and sampling effort instead of simply lists of species, maximizes the uses of these data.
- DNA barcoding/environmental DNA (eDNA) – with the rapidly decreasing costs of sequencing, genomic methods to measure communities will become increasingly important [95].
- Digital imaging – digital-imaging technology is allowing a step change in the coverage and frequency of biodiversity sampling through the use of camera traps, drones, and smartphones.
- Citizen science – social-media methods are increasingly making it possible to use censuses provided by laypeople with good confidence in the data quality.
- Remote sensing – the convergence of Lidar and hyperspectral methods with high resolutions should soon allow flyover surveys of at least canopy species.

Better coverage

Although existing data are not fully exploited, it is clear that they are insufficient to provide a complete picture of biodiversity change. Certain taxa, such as insects, and vast tracts of the Earth's surface, such as the terrestrial tropics and all marine habitats, are strongly underrepresented in biodiversity surveys.

Gaps in scales and trends

Figure 2 in main text highlights the gaps in knowledge about biodiversity change at different spatial and temporal scales. Synthesis and theory regarding change in these gaps is particularly urgent.

Research questions

Improve our understanding of temporal and spatial beta diversity

These have been relatively poorly studied topics to date, but appear central to understanding biodiversity trends.

Bridge from populations to communities

Better understanding of how individual species dynamics (winners and losers, colonization and extinction) are influenced by various human impacts and how they scale up to overall community trends in biodiversity.

Identify optimal metrics of biodiversity

Which metrics most reflect what humans value in biodiversity? (This question clearly requires collaboration with social scientists.)

Policy actions

(i) Develop institutions with responsibility for biodiversity at multiple scales. Most monitoring and management is at the local level. As Figure 2 in main text demonstrates, trends in local biodiversity are linked to trends in landscape and regional biodiversity, although the mechanisms involved are incompletely understood. A challenge is to enable policymakers and the public to take responsibility for local biodiversity in a way that is consistent with protecting biodiversity at the regional level. Ostrom [96] has identified this goal as a fundamental need in all natural resource management and calls them polycentric institutions.

(ii) Transition to managing dynamic equilibria. Biodiversity loss is widely reported, but the key message of this review – that change is complex, with both gains and losses occurring – is not widely appreciated. Often natural reserves are treated as static collections of species, rather like a collection of pictures in an art museum. The significance of the gains and losses needs to be interpreted in the regional context and local managers, in addition to reporting trends in iconic species, need to monitor the abundances of the species in the assemblage as well as overall trends in biomass and abundance.

(iii) Transition to managing different aspects of biodiversity. To date, conservation has been almost exclusively focused on single species or on α diversity (often species richness). α diversity is only one aspect of biodiversity and there is growing evidence that it may be one of the least sensitive indicators of the impact humans are having (see 'What we know about trends in α diversity').

(iv) Communicate the complexity to the public. If recommendations (i)–(iii) are to be followed by policymakers, it will be important to have a parallel effort to explain these changes by communicating that biodiversity is complex and multifaceted. One concrete example might be the need to have more discussion about winners and losers, and whether the current winners and losers are desirable from a human perspective, rather than simply about α diversity.

changes. Many trends are almost completely unstudied, including temporal and spatial β diversity and changes in net abundance at the community level. Additionally, for the credibility of future generations of biodiversity scientists, we also believe it is important to communicate the currently very large error bars in estimates of biodiversity trends.

A second striking fact that emerges is that, even faced with dramatic environmental change, species richness (α) can remain, on average, constant (see discussion of α-L and α-B and Box 3). However, this apparent constancy hides enormous turnover in the identities of the species present (see discussion of α-L, α-B, Tβ-L, and Tβ-B, Figure 3, and Boxes 2 and 3). One meta-analysis [12] suggests that 10% of species exit and are replaced by new species every decade. Evidence to date also suggests loss of spatial variation (declining spatial β diversity) is occurring. These patterns in temporal and spatial β diversity strongly suggest that: (i) signals of constant richness (α diversity) should not lead to complacency; (ii) we need to devote much more work to quantifying changes in community composition (temporal β diversity) and spatial structure (spatial β diversity); and (iii) we need to broaden our focus from simply the quantity of biodiversity to include the quality of biodiversity.

The switch to including quality of biodiversity alongside quantity is not a small change. It will require subjective discussions driven by diverse human values about what defines high-quality versus low-quality biodiversity. Many people already have intuitive notions of quality of biodiversity (e.g., more rats and jellyfish and fewer lynxes and tuna would be considered by many as a decrease in quality). However, quantifying and measuring the types of changes in species composition that are occurring will require work and additional definition (Table 1). Such discussion of quality of diversity and how this varies depending on which species are present is already implicit in conservation planning but needs to be brought to the fore and made an explicit goal.

Many citizens are untrained experts on patches of local biodiversity. Naturalists, gardeners, hunters and fishers, and outdoor enthusiasts spend time in nature and appreciate how biodiversity has changed in the areas they frequent. Few doubt that humans are causing massive changes in biodiversity and that changes in species composition are degrading biodiversity. As we have shown here, the simplest and best-known metrics of biodiversity (e.g., local and regional species richness) do not always capture these changes. Biodiversity scientists need to

Table 1. Attributes of quality of biodiversity

Aspect of quality of diversity[a]	Comment
Functional diversity	Evidence suggests that ecosystem function may be higher or more stable with greater functional diversity
Trait diversity	Closely related to functional diversity but this is increasingly being used as a measure of phenotypic diversity in a community
Phylogenetic diversity	More evolutionary history is conserved when phylogenetic diversity is higher
Genetic diversity	More alleles preserved in a community give greater phenotypic variation and a higher possibility of adaptive evolution
Anthrophiles versus anthrophobes	Some species are commonly associated with humans (e.g., crows, rats) and some avoid humans (e.g., wolves); the Anthropocene may be strongly filtering on this one trait
Rare versus common	Conservation biology is defined by some as the science of rarity (i.e., rare species)
Specialist versus generalist	Species that are highly specialized (i.e., narrow niche) are often deemed more in need of protection than generalists

[a]If increasing importance is placed on the quality of biodiversity in addition to the quantity, we need to define quality. Several ideas currently in the literature are related to the notion of quality of biodiversity, as summarized here.

acknowledge areas of ignorance (e.g., spatial and temporal β diversity) and report error bars and to begin discussions on defining and measuring the quality of biodiversity. We strongly believe that in the long term this will strengthen rather than weaken the position and credibility of biodiversity science in the policy arena and engender public engagement as we more accurately describe the changes everyone is observing in biodiversity in the Anthropocene.

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