LETTERS

A balance of winners and losers in the Anthropocene

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Abstract

Scientists disagree about the nature of biodiversity change. While there is evidence for widespread declines from population surveys, assemblage surveys reveal a mix of declines and increases. These conflicting conclusions may be caused by the use of different metrics: assemblage metrics may average out drastic changes in individual populations. Alternatively, differences may arise from data sources: populations monitored individually, versus whole-assemblage monitoring. To test these hypotheses, we estimated population change metrics using assemblage data. For a set of 23 241 populations, 16 009 species, in 158 assemblages, we detected significantly accelerating extinction and colonisation rates, with both rates being approximately balanced. Most populations (85%) did not show significant trends in abundance, and those that did were balanced between winners (8%) and losers (7%). Thus, population metrics estimated with assemblage data are commensurate with assemblage metrics and reveal sustained and increasing species turnover.

INTRODUCTION

Increases in human population size, resource use and fossil fuel consumption are a threat to global biodiversity. Populations can be classified as 'winners' or 'losers', according to whether they are thriving or declining in the midst of all these changes to the planet (McKinney & Lockwood 1999). Populations that are increasing or that successfully colonise an environment are defined as winners, whereas declining populations or populations that go locally extinct are considered losers. Changes in abundance (population trends) and occupancy (local extinctions and colonisations) are both important components of biodiversity change, and contribute in correlated but different ways to biotic change. Here, we compare the proportions of winners and losers in populations monitored in the recent past across the globe.

Most studies that have invoked the winners and losers framing suggest that losers greatly outnumber winners. For example, McKinney & Lockwood (1999) found 64% losers (declining populations), 14% winners and 22% stable or neutral populations in studies of human perturbations. An assessment of species trends across the UK also concluded that 60% of 3148 studied species had declined (Hayhow *et al.* 2016). Widespread declines in populations of vertebrates and invertebrates, drawn from global compilations of studies, have been interpreted as the world undergoing a process of 'defaunation' (Dirzo *et al.* 2014). The IUCN Red List species, which assigns species a status of conservation concern, is another widely used system. Species classified in categories of endangered to critically endangered are often presumed to be on their way to extinction (Ceballos *et al.* 2015), and increasing numbers of

species assigned to the threatened category are thought to reflect increasing numbers of losers (Butchart *et al.* 2006) (but see also (Daskalova *et al.* 2018)). At the global scale, for example, the Red List Index suggests increasing deterioration of the conservation status of birds (Butchart *et al.* 2004). The Living Planet Index (LPI) takes a geometric mean of temporal trends across many populations and species of vertebrates to get an overall mean trend (Loh *et al.* 2005) rather than individually identifying winners and losers. The most recent report of a decline of 58% in the LPI since 1970 (LPI 2018) provides further support for the view that losers dominate in the Anthropocene.

What these approaches have in common is that they pull together data on populations (and sometimes species) that have been monitored in isolation from the assemblage in which they are embedded. However, the widespread evidence for temporal declines in population-level metrics contrasts with conclusions reached using assemblage-level metrics. Assemblage-level approaches evaluate taxa that co-occur in a defined spatial context and summarise biodiversity data through measures such as species richness and total abundance. Each assemblage is typically sampled using a standardised sampling protocol applied consistently through time. Assemblage-focussed analyses provide evidence of balanced changes in both species richness and abundance through time (Vellend *et al.* 2013; Dornelas *et al.* 2014; Elahi *et al.* 2015; Hillebrand *et al.* 2018). In other words, long-term biodiversity monitoring of entire assemblages reveals heterogeneous trends in species richness and total abundance, with no evidence for consistent and widespread declines in species number or total abundance. How can the contrasting conclusions about

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biodiversity change emerging from assemblage-level and population-level analyses be reconciled?

Differing conclusions about biodiversity trends at population and assemblage levels may be driven by contrasts in the nature of the data they draw on, by the metrics themselves, or by both. It is not possible to calculate assemblage-level metrics from population monitoring data, but the reverse is feasible and can help resolve this question. We therefore use assemblage-level monitoring programs to evaluate the balance of winners and losers among their constituent populations. If these assemblage-level studies uncover an excess of losers, we can conclude that assemblage-level metrics, such as species richness, are insensitive to the widespread declines in populations that have been reported in analyses based on population-level data. However, low prevalence of within-assemblage losers would indicate that declines do not dominate assemblage dynamics. Moreover, any balance in the frequency of winners and losers would be consistent with community-level regulation (Gotelli *et al.* 2017). Given the dynamic nature of the species composition of assemblages (McArdle *et al.* 1990), we consider colonisations and extinctions, alongside population trends, in our examination of winners and losers.

A key difference between population-level and assemblage-level studies is the approach to sampling taxa. Assemblage-level studies aim to exhaustively sample all species within an assemblage, regardless of species overall abundance or conservation status. Of course, any sampling methodology is likely to have some bias for or against certain species. For example, daylight sampling is less likely to detect the presence of nocturnal species. However, if a sampling methodology is applied consistently through time, there should be no consistent bias in whether the abundance of a particular species is increasing or decreasing through time. In contrast, population monitoring is more targeted and hence better able to address species-specific detectability issues. However, population-level compilations do not represent a random selection of all species, and any bias in the criteria used to select species can lead to a bias in the estimate of the frequency of species with high extinction risk. For example, population monitoring programs may not be directed towards species that are common and occur reliably (they may be of little conservation or commercial interest). It is possible that this difference in how taxa are sampled is responsible for the discrepancies between studies based on assemblage-level and population-level monitoring.

An alternative explanation for the discrepancies is that assemblage-level metrics may be insensitive to profound underlying change of individual populations within the assemblage. Assemblage-level dynamics of ongoing extinction, colonisation and turnover could mask underlying trends in abundance or local extinction of individual species. Although assemblage-level data have so far not provided evidence for widespread declines in biodiversity, they have revealed a strong signal of change in species composition through time (Dornelas *et al.* 2014). Moreover, roughly half of these assemblages show evidence for community regulation of total species richness and abundance (Gotelli *et al.* 2017). In such assemblages, the trajectories of individual species may not show simple upward or downward trends, but repeated arrivals and disappearances and complex patterns of increasing and decreasing populations. For example, it is possible that many species have declining populations that have not yet gone extinct, and a few species are increasing substantially. These important changes would not be revealed by analyses of species richness or total abundance. By dissecting the patterns of colonisation, extinction and population trends in the assemblage data, we have a better chance of detecting long-term declines in abundance or increases in the rate of local extinctions. Such analyses should help resolve the conflict between observing widespread declines at the population level, but no net change on average at the assemblage level.

An ideal data set for this purpose would use either a uniform, random or stratified sampling process to select sites across the globe. Unfortunately, such a monitoring design has not been established and is unlikely to be in the near future (Primack *et al.* 2018). Hence, to tackle questions about biodiversity change across the globe, we must rely on data from compilations of individual ecological studies and monitoring efforts. Although we recognise that ecological research effort has been geographically biased (Martin *et al.* 2012; Gonzalez *et al.* 2016; Meyer *et al.* 2016; Vellend *et al.* 2017), this bias affects both population- and assemblage-level studies, and is ultimately driven by the geographic distribution of ecological effort.

In this paper, we ask whether we can detect a high prevalence of declining populations and accelerating extinction rates in assemblage-level data. Under our hypothesis that taxon sampling bias explains the differences found in population- and assemblage-level metrics, we should find a balance in population declines and increases, and constant and balanced rates of local colonisation and extinction. Conversely, if assemblage-level metrics mask widespread declines, we should uncover many more losers than winners, and accelerating extinction rates.

METHODS

Data

We used the largest database of long-term *in situ* monitoring of all species in an assemblage collected to date, the BioTIME database (Dornelas *et al.* 2018). In this analysis, we wanted to retain sufficient power to detect extinctions and colonisations, so we used only data sets with at least 10 years of data. The full list of studies used is included in the Supplementary Material. In total, this corresponds to 158 studies, containing a total of 16 009 species and 24 940 populations (we use the term population to refer to the abundance of each species in each study) of plants, invertebrates and vertebrates. Critically, every species detected in any of these studies was retained and analysed, so no filtering on species occurred.

We worked at two organisational scales: at the assemblage scale, we focused on detecting local extinctions and colonisations. At the population scale, we estimated long-term trends in abundance. Local extinctions can be thought of both as leading indicators of global extinction and as an extreme pattern of a declining population.

Colonisation and extinction rates

We took two distinct approaches to study colonisation and extinction. One approach assumed no detection errors and

defined a population extinction as a species presence in year (*t*) followed by the species absence in the following year (*t* + 1), and a population colonisation as a species absence in year (*t*) followed by the species presence in year (*t* + 1). We measured the aggregate extinction and colonisation rates as the proportion of species present that went extinct or colonised each year. We then calculated a linear trend of the extinction and colonisation probability over time, utilising an ordinary least squares regression, and used the slope of the trend as a measure of change in rates of extinction or colonisation. We also accounted for study differences, across all data sets, as a random effect (Bates *et al*. 2015).

Colonisation and extinction test

The second approach was more conservative and recognised that transitions between zero and non-zero could be due to detection errors as well as genuine colonisation or extinction events. Because we did not have repeated within-year visits to a site, we were unable to use standard detection models (Shimadzu *et al*. 2016). We first converted the population series to a binary presence–absence vector, which is an ordered sequence of 1 s and 0 s. If the ordering of 0 s and 1 s is random, the absences can be interpreted as detection errors (which are more likely when N is small), or ephemeral extinctions (which are followed by subsequent recolonisations). But if the 1 s and 0 s are aggregated in sequence, it suggests a non-random sequence of disappearances (if a long run of 1 s is followed by a run of 0 s) or appearances (if a long run of 0 s is followed by a run of 1 s). We first tested for non-random binary sequences using the 'runs.test' function in the 'tseries' library of R version 3.1.2 (R Core Team 2018). We tested only for aggregated sequences ('alternative = 'less'' option). Note that a significant test means that the run of 1 s (and therefore also of 0 s) is significantly longer than expected by chance, given the total length of the series and the number of presences and absences it contains. We verified that, even with a minimum time series length of $n = 10$, the test would detect a statistically significant pattern ($P < 0.05$) for the most extreme case (1000000000 or 0000000001; $P = 0.02275$). Although the runs test is not conclusive evidence of 'true' colonisation or extinction event (as opposed to a sustained detection error), we use that label for convenience here.

If the runs test detected a non-random pattern and the sequence contained only one colonisation (run of 0 s followed by run of 1 s), we called this a 'colonisation'. If the runs test detected a non-random pattern and the sequence contained only one extinction (run of 1 s followed by run of 0 s) we called it an 'extinction'. If the runs test detected a non-random pattern but contained multiple colonisations and extinctions, then we called it a 'multiple colonisation and extinction' series. If the runs test indicated a random sequence, we classified the population as 'persistent', which included both populations that were always present and populations with intermittent presences and absences over the time period. Thus, the second method of examining colonisations and extinctions helped us determine whether or not the sequences of 0 s and 1 s should be interpreted as colonisation or

extinction events. This allowed us to classify data into four categories: colonisation, extinction, multiple colonisation and extinctions, and persistent populations (Fig. 1).

Population trends (winners and losers)

We estimated population trends by fitting a linear regression to population abundances. We did not include the time when a species was absent (pre-colonisation or post-extinction) in the trend lines, because that would tend to flatten the slope towards zero. In single colonisation or extinction time series, the trend line was calculated only on the abundance data after the last zero or before the first zero respectively. In multiple colonisation time series, the trend was calculated across the first non-zero population to the last non-zero population. If the population was persistent, we calculated the trend line across the entire time series. Note that the last three methods included intermittent zeros in the trend lines.

With the data on which to calculate a trend line identified for each population, we first applied a square-root transformation to the population data. This transformation stabilises the variance and is appropriate for models in which population size is determined by some kind of Poisson process. This transformation accommodates 0 s and avoids the distortions that arise from a $\ln(x + 1)$ transformation (McArdle & Anderson 2001). Next, we used the 'scale' function in R to rescale each data set so that it had a mean of 0 and a standard deviation of 1. This transformation put all time series into common units that are more appropriate for comparisons of taxa with disparate body sizes, such as vertebrates and plankton. Finally, we fit an ordinary least squares regression line through the transformed data and calculated the slope and its statistical significance (one-tailed test). Note that *P*-values calculated in this way are identical to *P*-values that would be obtained before the scaling transformation. To explore possible explanations of the variations in the trends, we fitted mixed models with study ID as a random effect and classifications of the populations according to Taxon, Climatic band (Tropical, Temperate and Polar and combinations of these) and Realm (Marine, Terrestrial and Freshwater).

RESULTS

The distributions of extinction or colonisation rates are balanced and centred on zero (Fig. 2). Only 11 of the 158 communities exhibited significantly accelerating extinction rates, and these were balanced by 11 communities exhibiting significantly decelerations in extinction rates. For colonisation rates, 21 of the 158 communities exhibited significant acceleration, and 15 communities exhibited significant deceleration. However, collectively, we see evidence for subtle but significantly acceleration rates of both extinction (slope = 0.000713; SE = 0.000248; $P = 0.0042$) and colonisation (slope = 0.000548; SE = 0.000189; $P = 0.0039$) (Fig. 2).

The extinction and colonisation test resulted in a classification of populations. Across the four classifications (Fig. 1), 20.21% of the sequences were significant according to the runs test. These non-random sequences were split as 2.73% single extinctions, 5.19% single colonisations, and 12.28%
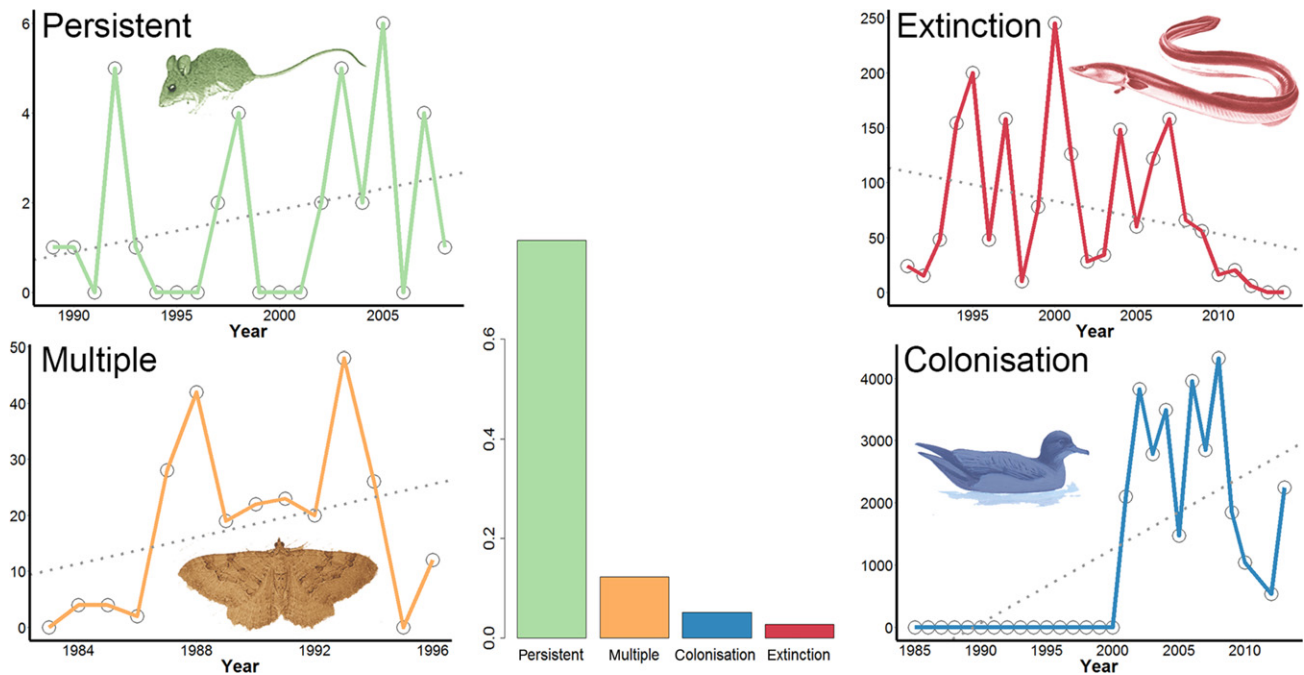
Figure 1 Centre: Proportion of populations classified as persistent, multiple, colonisation and extinction as per definitions in the methods. Side panels show illustrations of each type of populations for the following species: Cactus mouse *Peromyscus eremicus* (persistent); European eel *Anguilla anguilla* (extinction); Greater shearwater *Puffinus gravis* (colonisation); Scarce tissue moth *Rheumaptera cervinalis* (multiple).
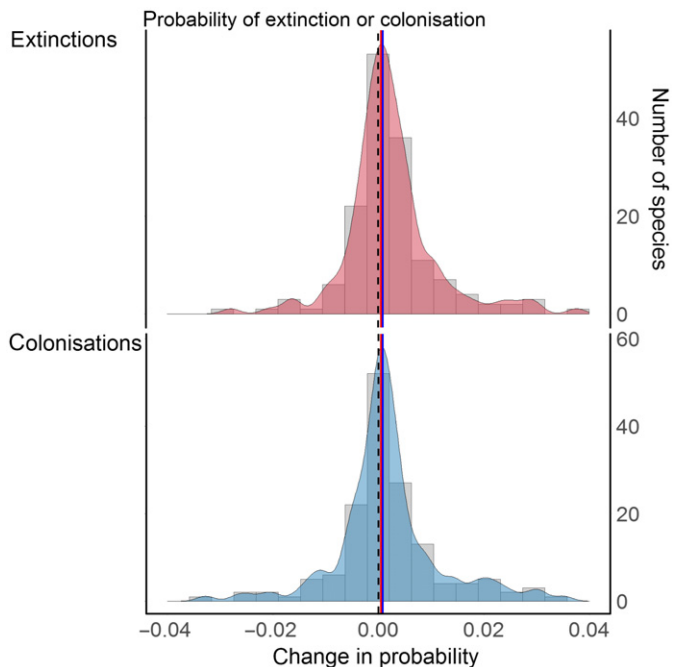

Figure 2 Density plots of the distribution of slopes of probability of extinction or colonisation through time. The dashed line marks a slope of 0, the red line the global slope for extinctions and the blue line the global slope for colonisations (from the mixed model).

multiple colonisations and extinctions. The remaining 79.80% sequences (random runs test) were classified as persistent. Population trends for these populations were remarkably variable, with all categories having both increasing and decreasing populations (Fig. 3). Nevertheless, there were clear and significant differences between the categories: both multiple colonisations and extinctions, and persistent populations centred on zero; populations going extinct had a higher proportion of decreasing populations; and colonising populations with a higher proportion of increasing populations.

As with the assemblage metric analysis, the distribution of population trends was symmetrical and centred on zero. Based on the statistical significance of the population linear models ($P < 0.05$), we classified all populations as 'winners' (2.80%), 'losers' (3.31%) and 'no-trenders' (93.87%). Very little of the variation in population trends could be attributed to Taxa (R^2 fixed effects 0.0041, Fig. 4), Climatic region (R^2 fixed effects 0.0007, Fig. 5) or Realm (R^2 fixed effects 0.0007, Fig. 6).

DISCUSSION

In summary, we found that the frequency of winners and losers in assemblages was roughly balanced for both occupancy and abundance change. Extinction and colonisation rates were both accelerating on average but at similar rates (Fig. 2). The rates of average acceleration were close to, but distinguishable from zero. Rates of average acceleration were not homogeneous across assemblages because our study included some time series that are accelerating and others that are decelerating in colonisation and extinction rate. A minority of the populations contained a local extinction or colonisation event (around 8% of all populations, Figs 1 and 3) with slightly more colonisations than extinctions. However, even single digit numbers are indicative of substantial and consistent change in species composition, the clearest signal that
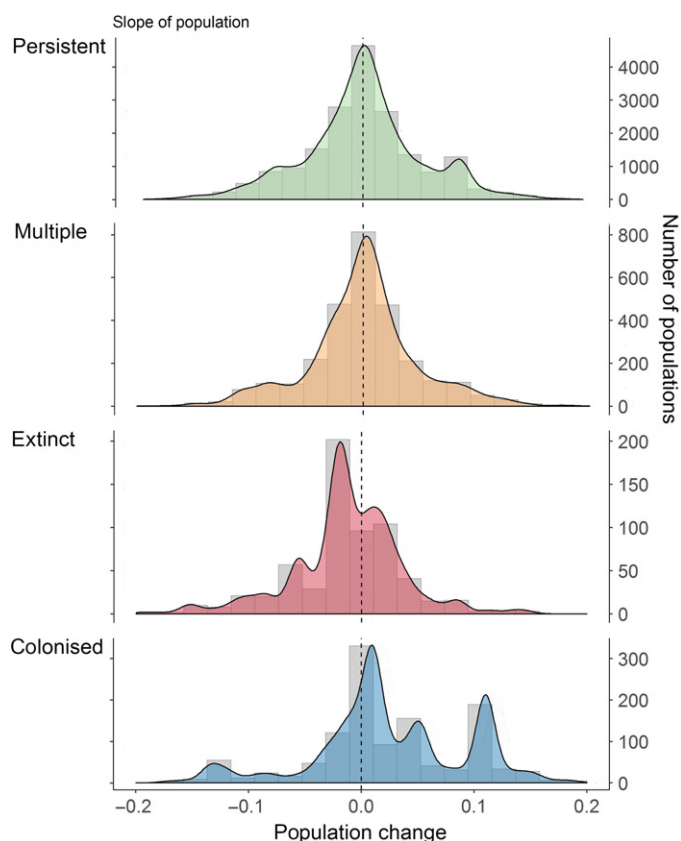
Figure 3 Density plots of the distribution of slopes of population size as a function of time for each type of population classified as per methods (see also Figure 1 for examples). The dashed line marks a slope of 0.

emerges from studies of biodiversity change in the recent past (Dornelas *et al.* 2014). In terms of population trends, the proportions of significantly increasing and decreasing populations were both around 3%, therefore being infrequent and approximately balanced among all populations. We could not detect population change in the vast majority of species. Therefore, using population-level metrics on assemblage-sampled data sets, we found population-level results that are consistent with the previously reported assemblage-level metrics. We previously found no net change in total assemblage abundance and species richness (Dornelas *et al.* 2014; Gotelli *et al.* 2017), here we report balanced increases and decreases in population trends.

These somewhat surprising results are in fact consistent with studies of a single group of organisms that report population-level metrics on assemblage-sampled data. These primarily come out of long-term monitoring studies such as national breeding bird surveys. For example, an analysis of long-term trends in the North American Breeding Bird Survey, which is one of 158 data sets included in our analysis, revealed a balance in which 49% of the populations of the species were increasing and the remaining 51% were decreasing (Sauer *et al.* 2003; Schipper *et al.* 2016). This paper explicitly analysed spatial and temporal heterogeneity of population trends within species and also found such heterogeneity to be very common. As such it was very easy to find specific regions and

specific subgroups of species which are declining, but necessarily other species and regions had increases to achieve a close balance of 49–51% overall increases/decreases. For the conservation goals of Sauer *et al.* (2003), it was appropriate to single out the declining populations, but for the larger goal of examining biodiversity trends, the message that winners and losers were evenly balanced was not highlighted. Similarly, a study of European Bird abundances (Inger *et al.* 2015) found that 74 populations were increasing and 70 decreasing (55 and 62 respectively being statistically significant). This study also found that rare species were increasing in abundance while common species were decreasing in abundance, with an overall net effect of decreasing total assemblage abundance [although this latter result is primarily accounted for by a single species, the house sparrow, which is highly abundant but experienced a decline for quite specific reasons (De Laet & Summers-Smith 2007)]. A study of coral cover (Edmunds *et al.* 2014) revealed that 32 genera of corals increased in relative abundance and 32 genera decreased in relative abundance, although again there was a finding of overall decline in total assemblage abundance. The same study found that increases and decreases of coral cover over palaeontological time was balanced and centred on zero. Although not classified at the species level, a global compilation of data on kelp forests found substantial variation in trends in kelp abundance that was centred close to, but significantly below, zero (i.e. a small preponderance of losers over winners). Even the State of Nature report on populations in the UK finds approximately 60% decreases in invertebrates and plants where only 4–6% of species are studied. However, in the one group where a majority of species were studied (58% of all vertebrates studied) almost 60% of species increased (were winners). Two large studies also of vertebrates, a very well-sampled group, found a balance between winners and losers at both the global and UK scales (Daskalova *et al.* 2018) or a slight overall preponderance of winners over losers in North America and Europe (Leung *et al.* 2017).

When total assemblages are sampled, or more generally when taxa are sampled comprehensively, the findings of population-level metrics disagree with those previously reported (McKinney & Lockwood 1999), but agree with previously reported assemblage-level metrics (Vellend *et al.* 2013; Dornelas *et al.* 2014; Supp & Ernest 2014). Clearly a pivotal issue is what fraction of the taxa are sampled and how they are chosen, and this appears to matter more than which exact subset of geographic data or taxa are used. A possible explanation is that there is bias in which populations have data available to include in studies such that data for declining populations become available more often than for increasing populations. If true, then any studies assembling these data would unintentionally have the same bias and explain the contrasting results discussed herein. There are at least three reasons to suspect that data on declining populations might be more readily available: bias to declining populations, bias to abundant populations and publication bias.

One reason we might gather more data on declining populations is selection bias – the populations we choose to study and collect data on might be biased towards preferentially selecting declining populations, for perfectly legitimate reasons. For
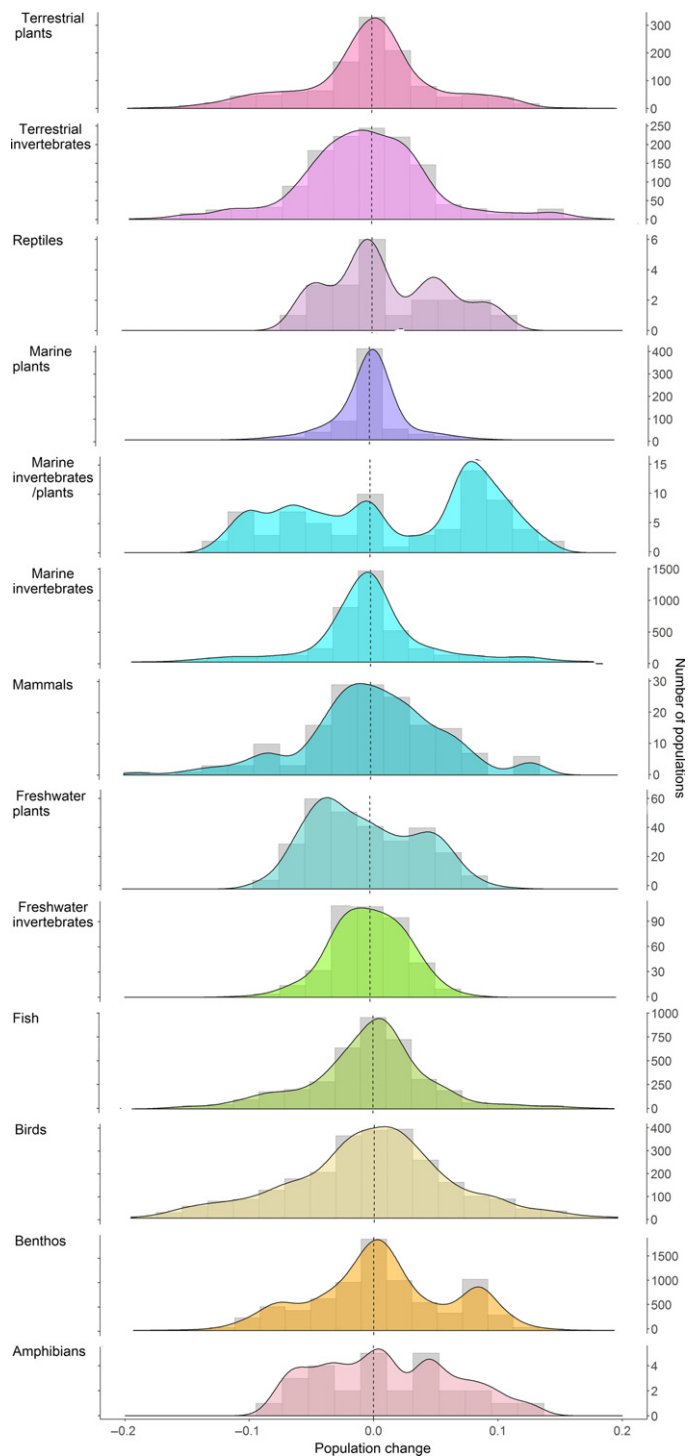
Figure 4 Density plots of the distribution of slopes of population size as a function of time for each taxon. The dashed line marks a slope of 0.

Figure 5 Density plots of the distribution of slopes of population size as a function of time for each climatic band. The dashed line marks a slope of 0.

example, government and conservation agencies are often mandated to monitor endangered populations. Similarly, populations that are being harvested such as fish or game are often monitored to assess the sustainability of the resource and prevent overexploitation. The only example we can think of that counterbalances this is that we often monitor populations of non-native species that are usually increasing, but these are
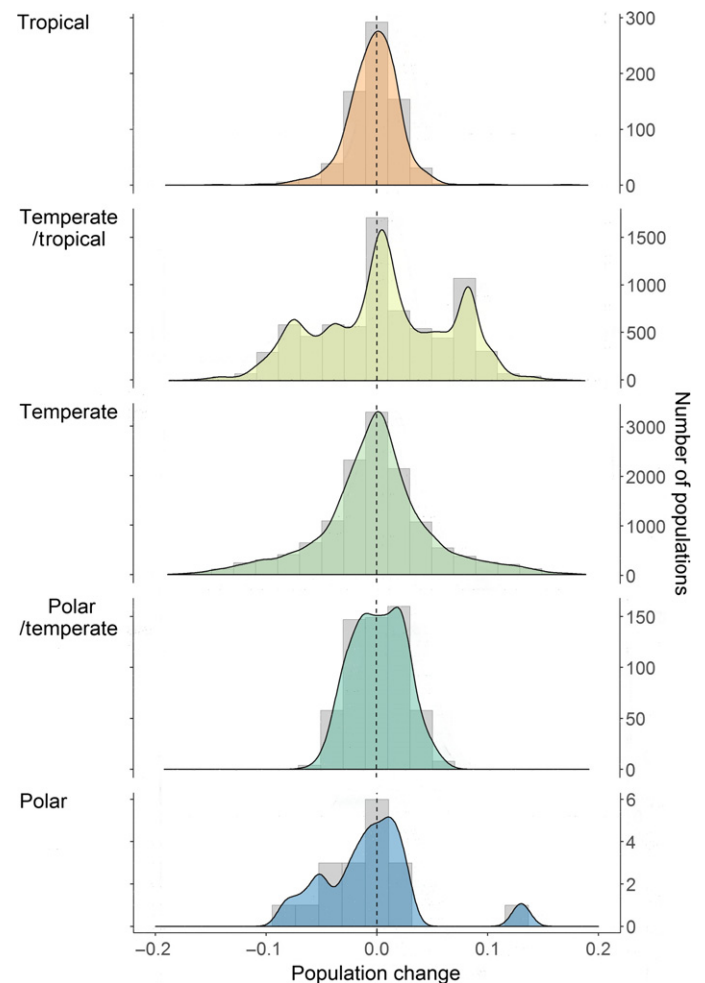
often explicitly excluded from winner and loser assessments. In this study, we did not exclude recent colonists, including non-native species.

A more subtle bias may occur among populations that are monitored for general scientific study rather than for specific conservation monitoring. In this case, ecologists may choose to start studying or monitoring populations that are above average in abundance for that species. Because most populations show large fluctuations in abundance, there may be a natural tendency to initiate studies with large, robust populations to ensure that there will be a population to study over the long term. This practical decision unintentionally selects for starting monitoring in populations that are well above their long-term mean even for the site (Heard 2016). As Pechmann *et al.* noted (Pechmann *et al.* 1991), 'Large populations may be more likely to be noticed or used by researchers. Anecdotal data therefore may be biased toward observing peak populations that eventually will decline, rather than the reverse'. To the extent that the relative abundance of species fluctuates this unintentionally results in picking species that are above their long-term relative abundance and are likely to decline.

The final reason to believe selection of populations may be biased is the well-known but poorly understood phenomenon
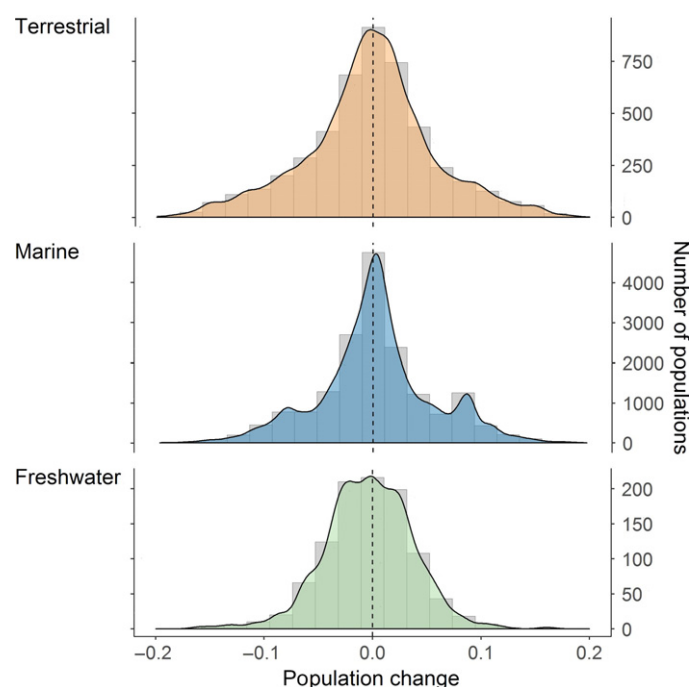
Figure 6 Density plots of the distribution of slopes of population size as a function of time for each realm. The dashed line marks a slope of 0.

of publication bias. The step from a researcher collecting to analysing and writing-up the data contains many filters on what is considered surprising, interesting and publishable. Even if an author deems a paper worth writing and submitting, journals may have filters on what is considered worth publishing. The occurrence and possible magnitude of publishing bias is widely recognised and many meta-analyses go to considerable effort to control for this problem (Parmesan *et al.* 2013; Gurevitch *et al.* 2018). We are aware of very few examples of tests for publication bias in studies that use population-level metrics and sampling for assessment of biodiversity. The only study that we are aware of that did test for publication bias showed signs of it (Newbold *et al.* 2015). But it seems quite credible that it is easier to publish a study warning about declining populations than a study showing no change or increasing populations.

We do not wish to imply that population monitoring data should not be used to assess biodiversity change. Indeed, because we cannot travel in time, any data about how the biosphere is changing in the Anthropocene are precious and should be used while being clear about the limitations of each data set, and the questions it can, or cannot, answer. With these points in mind, different sources of information should be combined to help us understand the complex ways in which the planet is changing. Investigating conflicting results, as we have done here, is highly informative, and allows us to identify strengths and weaknesses of different approaches to gain a more complete understanding of biodiversity change. By using multiple lines of evidence and seeking to identify patterns that are robust across approaches, we should be better placed to make informed decisions about how to manage the planet.

CONCLUSION

In this study, we show that population-level metrics of biodiversity using assemblage-sampled data give results consistent with previous assemblage-level metrics (Vellend *et al.* 2013; Dornelas *et al.* 2014; Supp & Ernest 2014) and inconsistent with previous studies using population-sampled data showing many more losers than winners (McKinney & Lockwood 1999) or drastic declines in average abundance indices (LPI 2018). We suggest that this difference is potentially due to the existence of biases towards data being more available for declining populations which will naturally bias any analysis of overall trends in population-level meta-analyses. Declining and increasing populations (winners and losers) are roughly equally balanced, but both groups are less common than populations showing little to no change. We find that extinctions and colonisations are also roughly balanced. Nevertheless, current rates of extinction and colonisation are orders of magnitude higher than null model predictions (Dornelas *et al.* 2014) and here we find evidence that they are both increasing. Therefore, biodiversity change is accelerating.

In short, the balance in winners and losers, and in extinctions and colonisations, suggests the two sides of gain and loss need to be considered simultaneously to determine ongoing biodiversity change. This has three main implications for moving forward in conservation. First, we need to significantly increase the effort and resources devoted to whole-assemblage sampling. Second, efforts towards ameliorating human impacts need to be directed towards specific populations (species and sites) that show strong declines and not predicated on an assumed but not well-documented scenario of losers badly outnumbering winners. Finally, the ongoing and accelerating replacement of species, reflected in accelerating rates of extinction and colonisation emerges as the most prevalent symptom of the Anthropocene.

AUTHORSHIP

AEM, BM, HS, MD and NJG designed the study. MD, HS and FM conducted analysis. BM and MD wrote the first draft, and all authors contributed to editing.

DATA ACCESSIBILITY STATEMENT

Data used in this study are listed in Supplementary table 1 and publicly available either through http://biotime.st-andrews.ac.uk or as described in supplementary table 1 and in the metadata table available through https://10.6084/m9.figshare.7687778.

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