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# 2 **A balance of winners and losers in**

# 3 **the Anthropocene**

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## **Abstract**

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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.

## 44 Introduction

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45  
46 Increases in human population size, resource use, and fossil fuel consumption are a threat  
47 to global biodiversity. Populations can be classified as “winners” or “losers”, according to  
48 whether they are thriving or declining in the midst of all these changes to the planet (McKinney  
49 & Lockwood 1999). Populations that are increasing or that successfully colonise an environment  
50 are defined as winners, whereas declining populations or populations that go locally extinct are  
51 considered losers. Changes in abundance (population trends) and occupancy (local extinctions  
52 and colonisations) are both important components of biodiversity change, and contribute in  
53 correlated but different ways to biotic change. Here, we compare the proportions of winners and  
54 losers in populations monitored in the recent past across the globe.

55 Most studies that have invoked the winners and losers framing suggest that losers greatly  
56 outnumber winners. For example (McKinney & Lockwood 1999) found 64% losers (declining  
57 populations), 14% winners, and 22% stable or neutral populations in studies of human  
58 perturbations. An assessment of species trends across the UK also concluded that 60% of 3,148  
59 studied species had declined (Hayhow *et al.* 2016). Widespread declines in populations of  
60 vertebrates and invertebrates, drawn from global compilations of studies, have been interpreted  
61 as the world undergoing a process of “defaunation” (Dirzo *et al.* 2014). The IUCN Red List  
62 species, which assigns species a status of conservation concern, is another widely used system.  
63 Species classified in categories of endangered to critically endangered are often presumed to be  
64 on their way to extinction (Ceballos *et al.* 2015), and increasing numbers of species assigned to  
65 the threatened category are thought to reflect increasing numbers of losers (Butchart *et al.* 2006)  
66 (but see also (Daskalova *et al.* 2018)). At the global scale, for example, the Red List Index  
67 suggests increasing deterioration of the conservation status of birds (Butchart *et al.* 2004). The  
68 Living Planet Index (LPI), takes a geometric mean of temporal trends across many populations  
69 and species of vertebrates to get an overall mean trend (Loh *et al.* 2005) rather than individually  
70 identifying winners and losers. The most recent report of a decline of 58% in the LPI since 1970  
71 (LPI 2018), provides further support for the view that losers dominate in the Anthropocene.

72 What these approaches have in common is that they pull together data on populations  
73 (and sometimes species) that have been monitored in isolation from the assemblage in which  
74 they are embedded. However, the widespread evidence for temporal declines in population-level  
75 metrics contrasts with conclusions reached using assemblage level metrics. Assemblage level

76 approaches evaluate taxa that co-occur in a defined spatial context and summarise biodiversity  
77 data through measures such as species richness and total abundance. Each assemblage is  
78 typically sampled using a standardized sampling protocol applied consistently through time.  
79 Assemblage-focussed analyses provide evidence of balanced changes in both species richness  
80 and abundance through time (Vellend *et al.* 2013; Dornelas *et al.* 2014; Elahi *et al.* 2015;  
81 Hillebrand *et al.* 2018). In other words, long-term biodiversity monitoring of entire assemblages  
82 reveals heterogeneous trends in species richness and total abundance, with no evidence for  
83 consistent and widespread declines in species number or total abundance. How can the  
84 contrasting conclusions about biodiversity change emerging from assemblage-level and  
85 population-level analyses be reconciled?

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

99         A key difference between population-level and assemblage level studies is the approach  
100 to sampling taxa. Assemblage level studies aim to exhaustively sample all species within an  
101 assemblage, regardless of a species overall abundance or conservation status. Of course, any  
102 sampling methodology is likely to have some bias for or against certain species. For example,  
103 daylight sampling is less likely to detect the presence of nocturnal species. However, if a  
104 sampling methodology is applied consistently through time, there should be no consistent bias in  
105 whether the abundance of a particular species is increasing or decreasing through time. In  
106 contrast, population monitoring is more targeted and hence better able to address species specific  
107 detectability issues. However, population level compilations do not represent a random selection

108 of all species, and any bias in the criteria used to select species can lead to a bias in the estimate  
109 of the frequency of species with high extinction risk. For example, population monitoring  
110 programs may not be directed towards species that are common and occur reliably (they may be  
111 of little conservation or commercial interest). It is possible that this difference in how taxa are  
112 sampled is responsible for the discrepancies between studies based on assemblage-level and  
113 population-level monitoring.

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

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

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

## 145 **Methods**

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### 146 ***Data***

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

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

### 158 ***1) Colonisation and extinction rates***

159 We took two distinct approaches to study colonisation and extinction. One approach  
160 assumed no detection errors and defined a population extinction as a species presence in year ( $t$ )  
161 followed by the species absence in the following year ( $t + 1$ ), and a population colonisation as a  
162 species absence in year ( $t$ ) followed by the species presence in year ( $t + 1$ ). We measured the  
163 aggregate extinction and colonisation rates as the proportion of species present that went extinct  
164 or colonised each year. We then calculated a linear trend of the extinction and colonisation  
165 probability over time, utilising an ordinary least squares regression, and used the slope of the  
166 trend as a measure of change in rates of extinction or colonisation. We also accounted for study  
167 differences, across all datasets, as a random effect (Bates *et al.* 2015).

## 168 **2) Colonisation and extinction test**

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

187 If the runs test detected a non-random pattern and the sequence contained only one  
188 colonisation (run of 0s followed by run of 1s) we called this a "colonisation". If the runs test  
189 detected a non-random pattern and the sequence contained only one extinction (run of 1s  
190 followed by run of 0s) we called it an "extinction". If the runs test detected a non-random pattern  
191 but contained multiple colonisations and extinctions, then we called it a "multiple colonisation  
192 and extinction" series. If the runs test indicated a random sequence we classified the population  
193 as "persistent", which included both populations that were always present and populations with  
194 intermittent presences and absences over the time period. Thus, the second method of examining  
195 colonisations and extinctions helped us determine whether or not the sequences of 0s and 1s  
196 should be interpreted as colonisation or extinction events. This allowed us to classify data into  
197 four categories: colonisation, extinction, multiple colonisation and extinctions, and persistent  
198 populations (Figure 1).

### 3) 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 0s 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

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The distributions of **extinction or colonisation rates** are balanced and centred on zero (Figure 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 Std

230 Error=0.000248,  $p=0.0042$ ) and colonisation (slope=0.000548 Std Error=0.000189,  $p=0.0039$ )  
231 (Figure 2).

232 The **extinction and colonization test** resulted in a classification of populations. Across  
233 the four classifications (Figure 1), 20.21% of the sequences were significant according to the  
234 runs test. These non-random sequences were split as 2.73% single extinctions, 5.19% single  
235 colonisations, and 12.28% multiple colonisations and extinctions. The remaining 79.80%  
236 sequences (random runs test) were classified as persistent. **Population trends** for these  
237 populations were remarkably variable, with all categories having both increasing and decreasing  
238 populations (Figure 3). Nevertheless, there were clear and significant differences between the  
239 categories: both multiple colonisations and extinctions, and persistent populations centered on  
240 zero; populations going extinct had a higher proportion of decreasing populations; and colonising  
241 populations with a higher proportion of increasing populations.

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

## 248 **Discussion**

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249 In summary, we found that the frequency of winners and losers in assemblages was  
250 roughly balanced for both occupancy and abundance change. Extinction and colonisation rates  
251 were both accelerating on average but at similar rates (Figure 2). The rates of average  
252 acceleration were close to, but distinguishable from zero. Rates of average acceleration were not  
253 homogeneous across assemblages because our study included some time series that are  
254 accelerating and others that are decelerating in colonisation and extinction rate. A minority of the  
255 populations contained a local extinction or colonisation event (around 8% of all populations,  
256 Figures 1 and 3) with slightly more colonisations than extinctions. However, even single digit  
257 numbers are indicative of substantial and consistent change in species composition, the clearest  
258 signal that emerges from studies of biodiversity change in the recent past (Dornelas et al 2014).  
259 In terms of population trends, the proportions of significantly increasing and decreasing  
260 populations were both around 3%, therefore being infrequent and approximately balanced

261 amongst all populations. We could not detect population change in the vast majority of species.  
262 Therefore, using population-level metrics on assemblage-sampled datasets we found population-  
263 level results that are consistent with the previously reported assemblage level metrics. We  
264 previously found no net change in total assemblage abundance and species richness (Dornelas et  
265 al 2014, Gotelli et al. 2017), here we report balanced increases and decreases in population  
266 trends.

267         These somewhat surprising results are in fact consistent with studies of a single group of  
268 organisms that report population-level metrics on assemblage-sampled data. These primarily  
269 come out of long-term monitoring studies such as national breeding bird surveys. For example,  
270 an analysis of long-term trends in the North American Breeding Bird Survey, which is one of  
271 158 datasets included in our analysis, revealed a balance in which 49% of the populations of the  
272 species were increasing and the remaining 51% were decreasing (Sauer *et al.* 2003; Schipper *et*  
273 *al.* 2016). This paper explicitly analysed spatial and temporal heterogeneity of population trends  
274 within species and also found such heterogeneity to be very common. As such it was very easy to  
275 find specific regions and specific subgroups of species which are declining, but necessarily other  
276 species and regions had increases to achieve a close balance of 49-51% overall  
277 increases/decreases. For the conservation goals of Sauer et al. (2003), it was appropriate to single  
278 out the declining populations, but for the larger goal of examining biodiversity trends, the  
279 message that winners and losers were evenly balanced was not highlighted. Similarly, a study of  
280 European Bird abundances (Inger *et al.* 2015) found that 74 populations were increasing and 70  
281 decreasing (55 and 62 respectively being statistically significant). This study also found that rare  
282 species were increasing in abundance while common species were decreasing in abundance, with  
283 an overall net effect of decreasing total assemblage abundance [although this latter result is  
284 primarily accounted for by a single species, the house sparrow, which is highly abundant but  
285 experienced a decline for quite specific reasons (De Laet & Summers-Smith 2007)]. A study of  
286 coral cover (Edmunds *et al.* 2014) revealed that 32 genera of corals increased in relative  
287 abundance and 32 genera decreased in relative abundance, although again there was a finding of  
288 overall decline in total assemblage abundance. The same study found that increases and  
289 decreases of coral cover over paleontological time was balanced and centered on zero. Although  
290 not classified at the species level, a global compilation of data on kelp forests found substantial  
291 variation in trends in kelp abundance that was centered close to, but significantly below, zero  
292 (i.e. a small preponderance of losers over winners). Even the State of Nature report on

293 populations in the UK finds approximately 60% decreases in invertebrates and plants where only  
294 4-6% of species are studied. However, in the one group where a majority of species were studied  
295 (58% of all vertebrates studied) almost 60% of species increased (were winners). Two large  
296 studies also of vertebrates, a very well-sampled group, found a balance between winners and  
297 losers at both the global and UK scales (Daskalova *et al.* 2018) or a slight overall preponderance  
298 of winners over losers in North America and Europe (Leung *et al.* 2017).

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

311         One reason we might gather more data on declining populations is selection bias – the  
312 populations we choose to study and collect data on might be biased towards preferentially  
313 selecting declining populations, for perfectly legitimate reasons. For example, government and  
314 conservation agencies are often mandated to monitor endangered populations. Similarly,  
315 populations that are being harvested such as fish or game are often monitored to assess the  
316 sustainability of the resource and prevent overexploitation. The only example we can think of  
317 that counterbalances this is that we often monitor populations of non-native species that are  
318 usually increasing, but these are often explicitly excluded from winner and loser assessments. In  
319 this study we did not exclude recent colonists, including non-native species.

320         A more subtle bias may occur among populations that are monitored for general scientific  
321 study rather than for specific conservation monitoring. In this case, ecologists may choose to  
322 start studying or monitoring populations that are above average in abundance for that species.  
323 Because most populations show large fluctuations in abundance, there may be a natural tendency  
324 to initiate studies with large, robust populations to ensure that there will be a population to study

325 over the long term. This practical decision unintentionally selects for starting monitoring in  
326 populations that are well above their long-term mean even for the site (Heard 2016). As  
327 Pechmann et al noted (Pechmann *et al.* 1991), “Large populations may be more likely to be  
328 noticed or used by researchers. Anecdotal data therefore may be biased toward observing peak  
329 populations that eventually will decline, rather than the reverse”. To the extent that the relative  
330 abundance of species fluctuates this unintentionally results in picking species that are above their  
331 long term relative abundance and are likely to decline.

332         The final reason to believe selection of populations may be biased is the well-known but  
333 poorly understood phenomenon of publication bias. The step from a researcher collecting to  
334 analyzing and writing-up the data contains many filters on what is considered surprising,  
335 interesting and publishable. Even if an author deems a paper worth writing and submitting,  
336 journals may have filters on what is considered worth publishing. The occurrence and possible  
337 magnitude of publishing bias is widely recognized and many meta-analyses go to considerable  
338 effort to control for this problem (Parmesan *et al.* 2013; Gurevitch *et al.* 2018). We are aware of  
339 very few examples of tests for publication bias in studies that use population-level metrics and  
340 sampling for assessment of biodiversity. The only study that we are aware of that did test for  
341 publication bias showed signs of it (Newbold *et al.* 2015). But it seems quite credible that it is  
342 easier to publish a study warning about declining populations than a study showing no change or  
343 increasing populations.

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

354 **Conclusion**

355 In this study, we show that population-level metrics of biodiversity using assemblage-  
356 sampled data give results consistent with previous assemblage level metrics (Vellend *et al.* 2013;  
357 Dornelas *et al.* 2014; Supp & Ernest 2014) and inconsistent with previous studies using  
358 population-sampled data showing many more losers than winners (McKinney & Lockwood  
359 1999) or drastic declines in average abundance indices (LPI 2018). We suggest that this  
360 difference is potentially due to the existence of biases towards data being more available for  
361 declining populations which will naturally bias any analysis of overall trends in population-level  
362 meta-analyses. Declining and increasing populations (winners and losers) are roughly equally  
363 balanced, but both groups are less common than populations showing little to no change. We  
364 find that extinctions and colonisations are also roughly balanced. Nevertheless, current rates of  
365 extinction and colonization are orders of magnitude higher than null model predictions (Dornelas  
366 *et al.* 2014) and here we find evidence that they are both increasing. Therefore, biodiversity  
367 change is accelerating.

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

377

378 **Figure captions**

379

380 **Figure 1** – Centre: Proportion of populations classified as persistent, multiple,  
381 colonisation and extinction as per definitions in the methods. Side panels show illustrations of  
382 each type of populations for the following species: Cactus mouse *Peromyscus eremicus*  
383 (persistent); European eel *Anguilla anguilla* (extinction); Greater shearwater *Puffinus gravis*  
384 (colonisation); Scarce tissue moth *Rheumaptera cervinalis* (multiple).

385

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

389

390 **Figure 3** – Density plots of the distribution of slopes of population size as a function of  
391 time for each type of population classified as per methods (see also Figure 1 for examples). The  
392 dashed line marks a slope of 0.

393

394 **Figure 4** – Density plots of the distribution of slopes of population size as a function of  
395 time for each taxon. The dashed line marks a slope of 0

396

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

399

400 **Figure 6** - Density plots of the distribution of slopes of population size as a function of  
401 time for each realm. The dashed line marks a slope of 0.

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414

415           **Data Accessibility statement**

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

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420           **References**

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