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A balance of winners and losers in the Anthropocene

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28   **Abstract**

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30   Scientists disagree about the nature of biodiversity change. While there is evidence for

31   widespread declines from population surveys, assemblage surveys reveal a mix of declines and

32   increases. These conflicting conclusions may be caused by the use of different metrics:

33   assemblage metrics may average out drastic changes in individual populations. Alternatively,

34   differences may arise from data sources: populations monitored individually, versus whole-

35   assemblage monitoring. To test these hypotheses, we estimated population change metrics using

36   assemblage data. For a set of 23,241 populations, 16,009 species, in 158 assemblages, we

37   detected significantly accelerating extinction and colonisation rates, with both rates being

38   approximately balanced. Most populations (85%) did not show significant trends in abundance,

39   and those that did were balanced between winners (8%) and losers (7%). Thus, population

40   metrics estimated with assemblage data are commensurate with assemblage metrics and reveal

41   sustained and increasing species turnover.

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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 3,148 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

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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.

Methods

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Data

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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.

1)Colonisation and extinction rates

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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).

199   ### *3)Population trends (winners and losers)*

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

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

223   ## Results

224   The distributions of **extinction or colonisation rates** are balanced and centred on zero
225   (Figure 2). Only 11 of the 158 communities exhibited significantly accelerating extinction rates,
226   and these were balanced by 11 communities exhibiting significantly decelerations in extinction
227   rates. For colonisation rates, 21 of the 158 communities exhibited significant acceleration, and 15
228   communities exhibited significant deceleration. However, collectively, we see evidence for
229   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).

Discussion

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.

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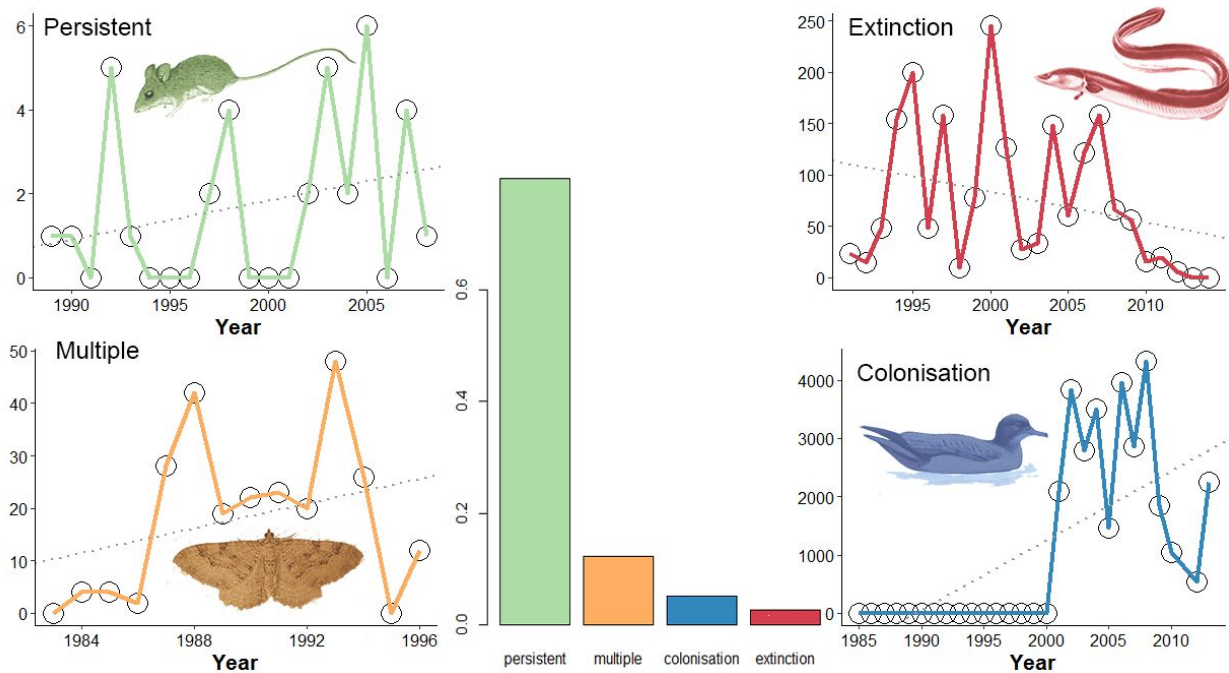
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Figure 1 – Centre: Proportion of populations classified as persistent, multiple,
colonisation and extinction as per definitions in the methods. Side panels show illustrations of
each type of populations for the following species: Cactus mouse *Peromyscus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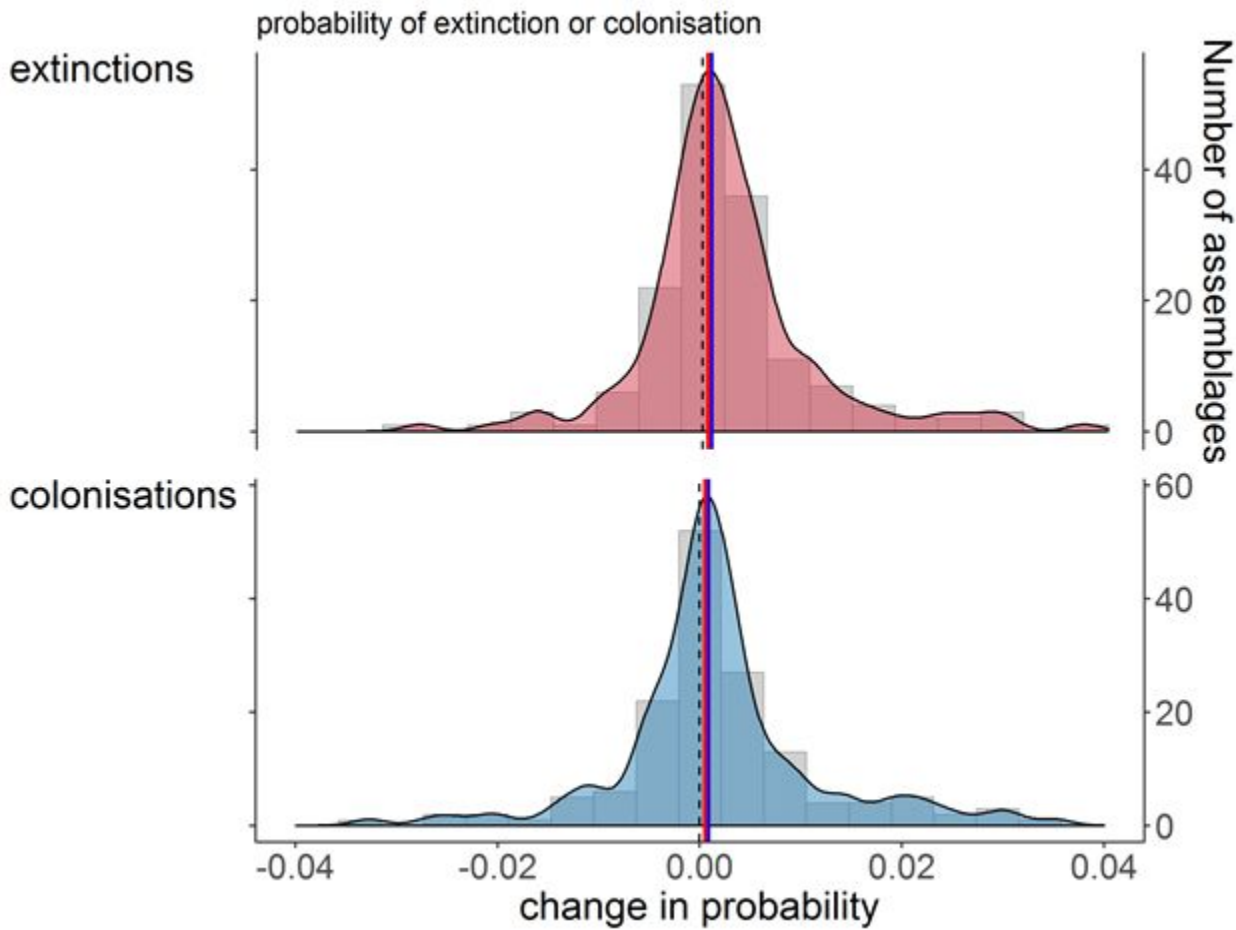(colonisation); Scarce tissue moth *Rheumaptera cervinalis* (multiple).

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39   402   **Figure 2** – Density plots of the distribution of slopes of probability of extinction or
40   403   colonisation through time. The dashed line marks a slope of 0, the red line the global slope for
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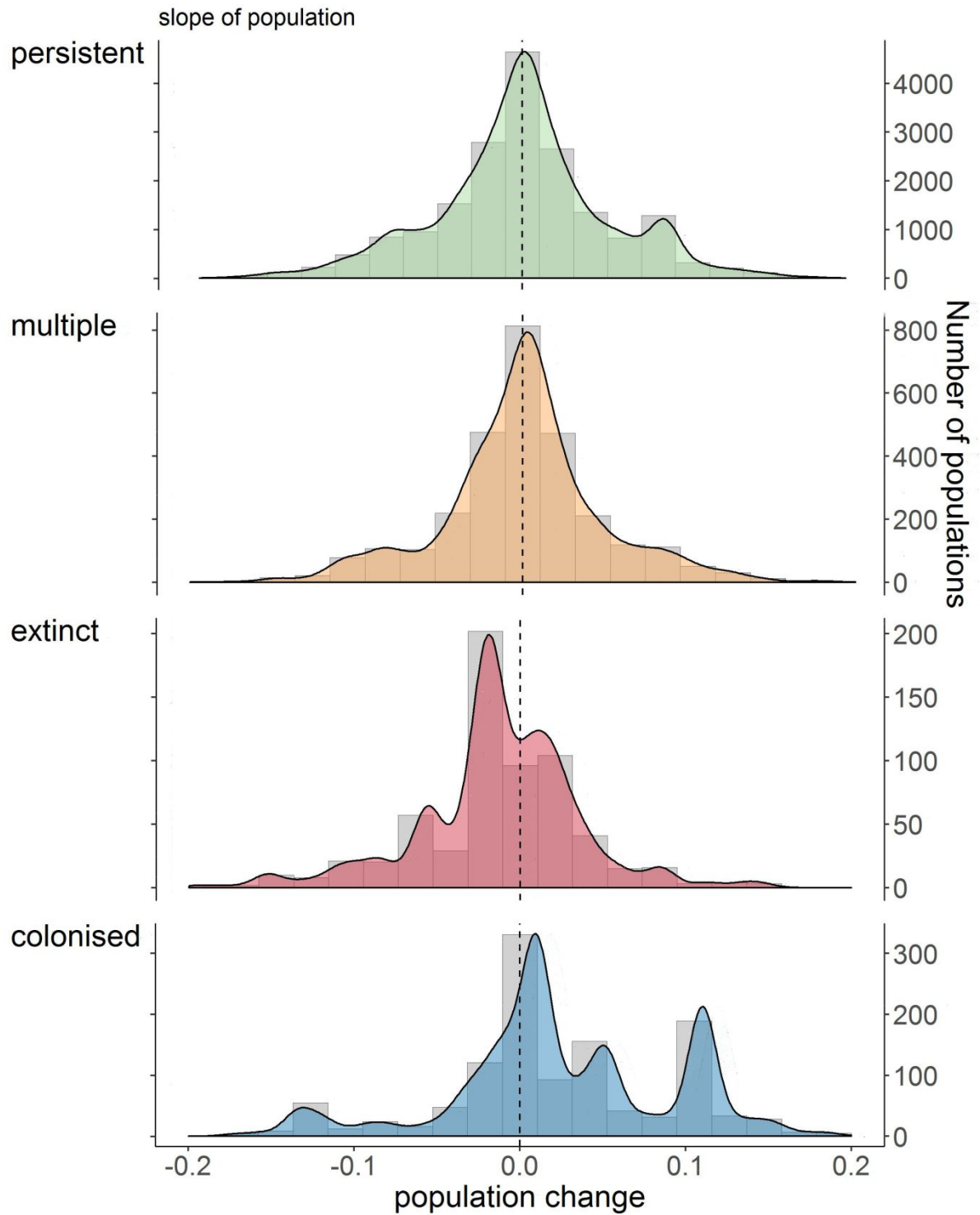42   404   extinctions and the blue line the global slope for colonisations (from the mixed model).
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Figure 3 – Density plots of the distribution of slopes of population size as a function of time for each type of population classified as per methods (see also Figure 1 for examples). The dashed line marks a slope of 0.
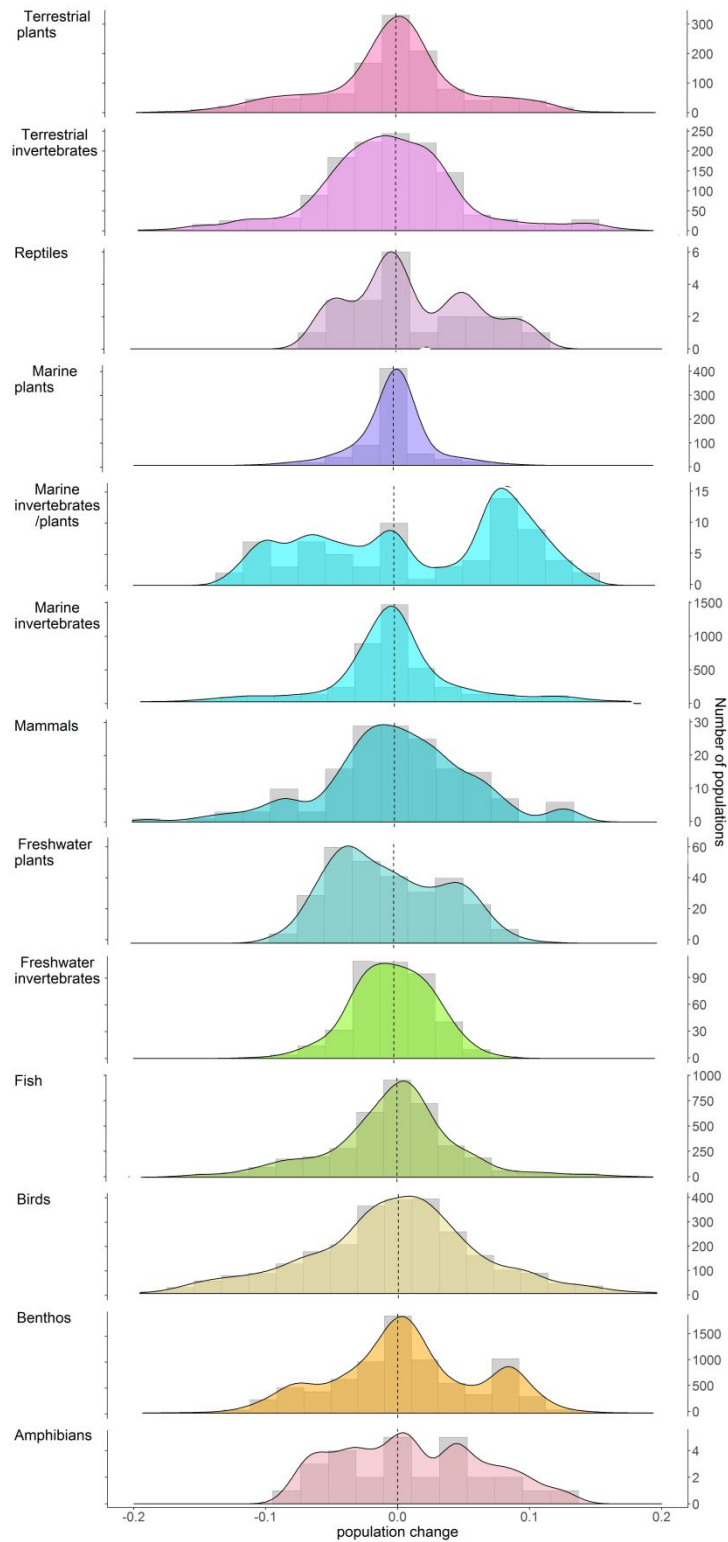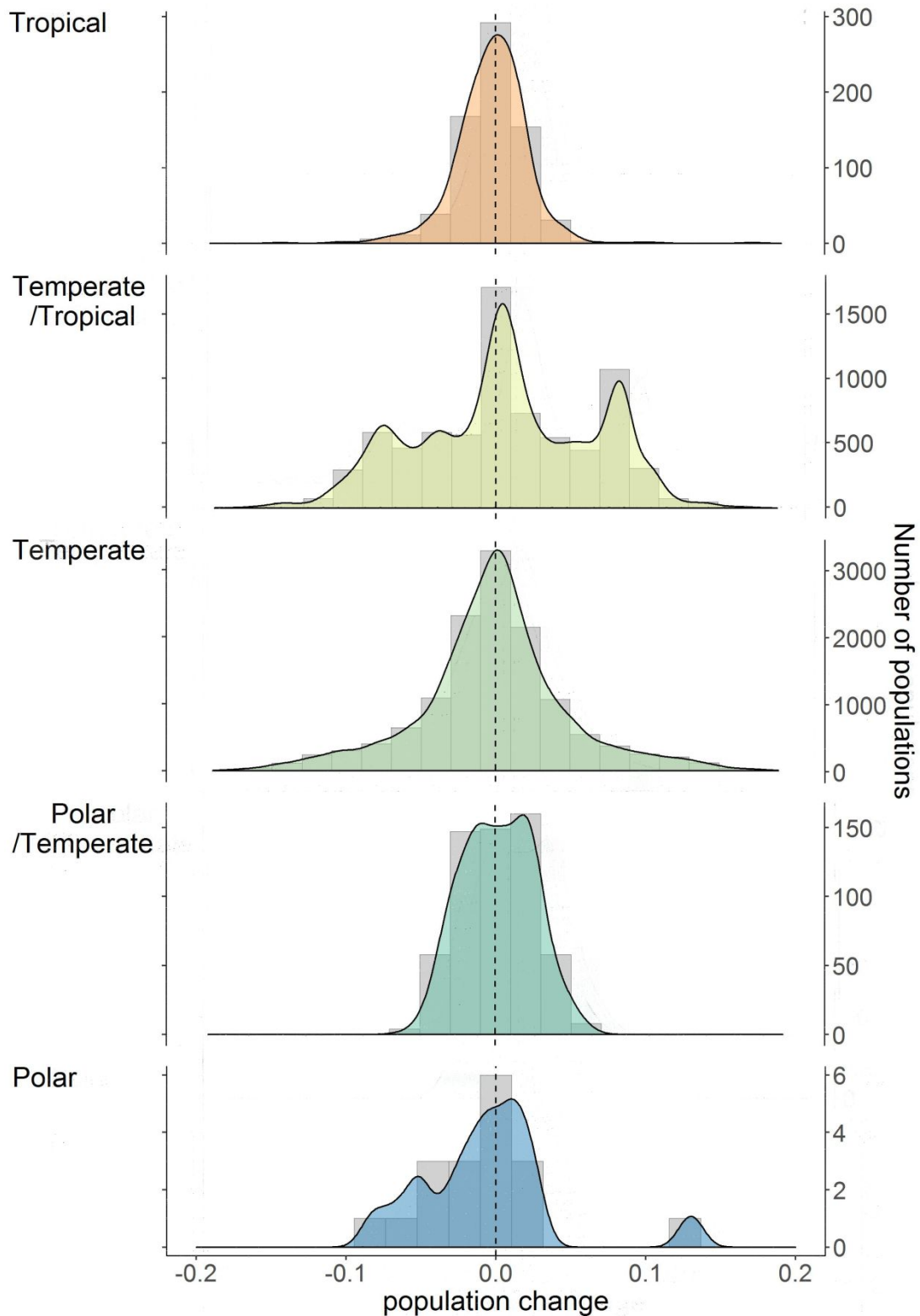
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Figure 4 – Density plots of the distribution of slopes of population size as a function of time for each taxon. The dashed line marks a slope of 0

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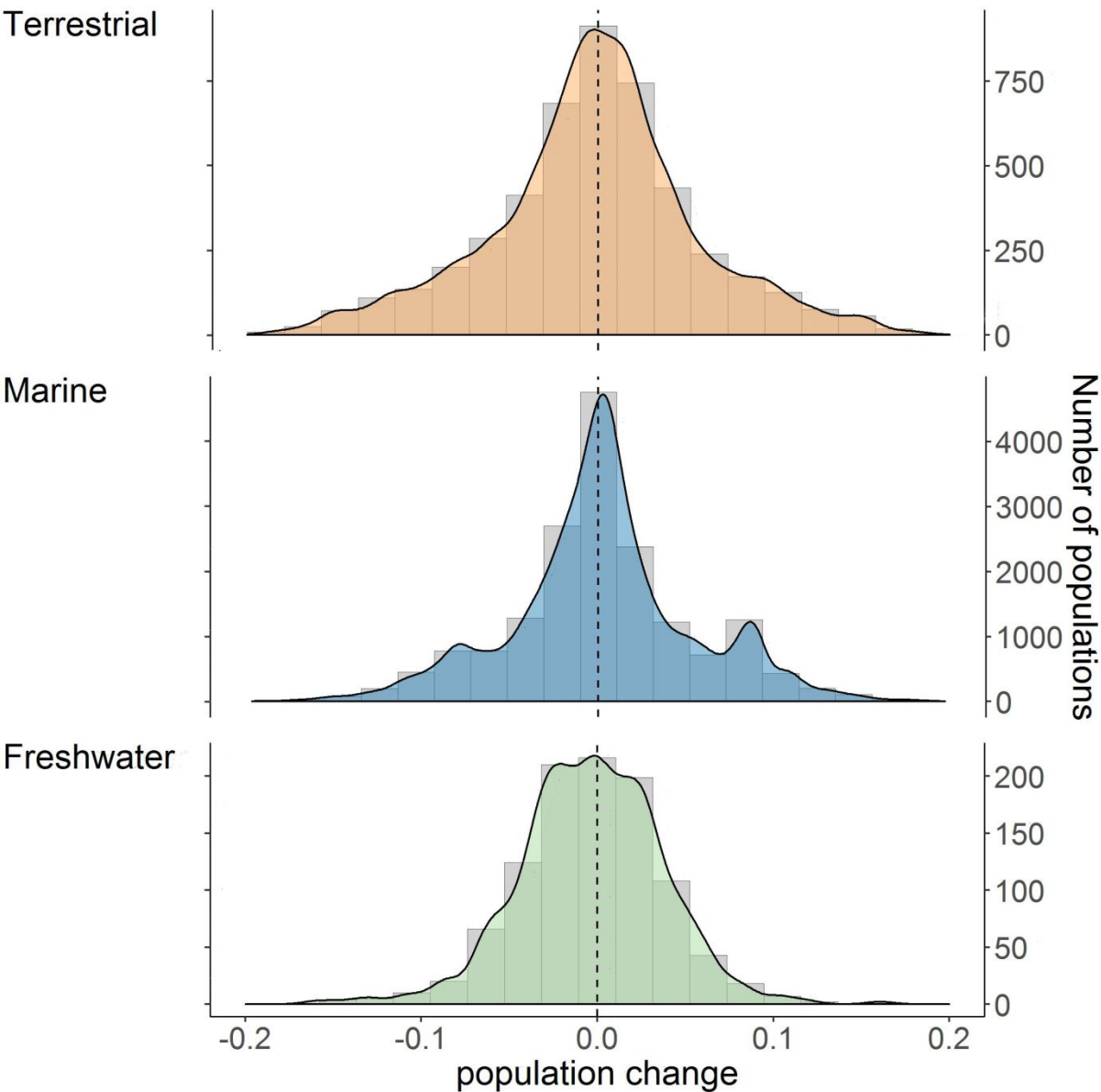
Figure 6 - Density plots of the distribution of slopes of population size as a function of time for each realm. The dashed line marks a slope of 0.

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