No pervasive size trend in global community dynamics.

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While recent meta- analyses have suggested that local taxonomic richness has on average remained invariant, potential shifts in functional traits remain underexplored at global scales. Here, by linking the largest cross-taxa community time series database to multiple trait databases, we show that within communities there is no clear trend between size traits and changes in abundance rank over time. This suggests that there is no pervasive tendency across biomes for larger species to be doing proportionally better or worse than smaller species.

Recent analyses have found that despite high and increasing levels of community turnover, there is no clear overall trend in the local-scale species richness[1–4]. However, it remains unclear how this result translates into functional changes. One of the most fundamental functional traits of a species is its size[5,6] and there is an expectation that a warming climate is will likely favour smaller bodysizes[7,8]. Further, larger species have been more extinction prone during some previous mass-extinctions[9,10], are more likely to show strong recent population declines[11], and (although relationships are threat-dependent) tend to be assessed at a higher risk of extinction[12] due to longer generational intervals and increased threat from habitat fragmentation and hunting[13].

One might therefore expect a detectable signal of shifts in community trait values beneath the apparent underlying consistency in taxonomic diversity. To examine this, we tested whether the body size of a species is correlated to a relative change in abundance through time using the publicly available BioTIME database[14]. This database is the largest collection of time series of ecological communities and has wide geographic and taxonomic scope[14]. After cleaning and standardising the names associated with the records, we linked six fundamental 'size' traits from four openly accessible trait databases representing four guilds – adult body mass from a database of amniote life history traits[15], adult body length and qualitative body size of marine species from the WoRMS database[16], plant maximum height and seed mass from the TRY database[17], and maximum body length of fish from a compilation[18] based on data in the FishBase repository[19].

Observations from single-location studies were collated, while widely dispersed studies were separately binned into a global grid of cells, each approximately 10km wide, and data from each study and cell were treated as discrete assemblages, following previous analyses[1,20]. Selecting only assemblages with quantified observations of ≥10 species, over ≥5 years, and with ≥40% of the species having records for at least one trait, we generated 22,915 community time series from 167 studies. This filtered dataset represented 2,516,175

36   observations of 12,033 species, of which 8,238 could be linked to at least one 'size' trait (representing 84.6% of

37   observations). Equally weighting studies, the average time series length was 17.2 years (range 5-70.5) and the

38   average number of species per included assemblage was 56.7 (range 10-337).

39   To focus on changes within the community and mitigate the risk of issues with changing sampling intensities

40   through time, for each trait and community assemblage time series for which there was sufficient data, we

41   calculated 'τ' - the Kendall rank correlation coefficient between the trait in question and change in relative-

42   rank of the abundance of each species within the assemblage (Fig 1a). This gives a non-parametric measure of

43   whether larger species are more or less likely than smaller species to have increased their relative rank

44   through time and, importantly, can be calculated where trait values for only a fraction of the observed species

45   are available. To weight each study within BioTIME equally, where there were multiple assemblages per study

46   these were averaged to generate a τ value for each possible study-trait combination. In order to provide a null-

47   model against which to evaluate the statistical significance of this multistage analysis, we repeated the

48   procedure with 100 trait randomisations per assemblage.

49   For five of the six tested size traits the distribution of study τ values was not significantly different from the

50   null model (Fig. 2, Extended Data Table 1). The one exceptional trait (amniote body mass) showed an overall

51   average positive relationship between size and relative abundance trends. Possible confounding factors for the

52   value of τ associated with each study, namely the total span of the time series, the number of sample points,

53   the species richness, the average trait completeness, the number of assemblages within the study, the grain of

54   the study and the absolute latitude did not consistently predict τ (Extended Data Figure 1, Tables 2-3).

55   These results indicate that there is not yet evidence for widely pervasive trends in a core functional trait, body

56   size. Importantly however, this study should not be seen as a refutation of the enhanced threats faced by the

57   very largest apex species[21]. Rather, against a background of considerable turnover[2,3] across the whole

58   community assemblage, on average, species positions in communities are being taken up by species of

59   comparable size. This suggests that previously identified shifts towards smaller species found in some

60   systems[7,22] may not be as universal as currently expected[8] and aligns with the divergent changes in global

61   body-size abundance distributions observed between mammal guilds[23]. However, we note that the variance in

62   τ across the dataset was consistently larger than that generated by a null model randomising the available trait

63   data within assemblages (Fig 2). This implies that many individual communities are experiencing significant

64   directional change in their body size traits, rather than local stasis or indeed active regulation.

65   The overall positive association across the amniote studies could have a number of causes that would benefit

66   from further investigation. One putative explanation is that anthropogenic dispersal limitations (generally

67   considered to act more strongly against smaller species) may be having a greater immediate impact than

68   climate change[24]. There are also indications of differences between terrestrial and marine systems. Previous

69   work with the same datasets[1,20] has found greater species richness and abundance changes in marine systems

70   than in terrestrial systems, while here we see a signal of greater trait-changes in the (largely terrestrial)

71   amniotes. In our study, the fish lengths trait displayed a distinctive distribution of τ (Fig 2c), with a modal peak

72   of studies showing small negative values, and then a tail of strongly positive relationships. This guild is also the

73   most likely to have experienced sustained anthropogenic pressure[25] and many of the 'fish' datasets in BioTIME

74   include data from surveys of actively fished and managed areas. Accurately quantifying marine community

75   trends is a challenge [26,27], but this distinctive pattern could be tentatively interpreted as a signal of the

76   imposition or relaxation of anthropogenic pressure across marine systems[28,29].

77   Our analysis necessarily sacrifices fine resolution for global scale. Although the lack of consistent study-level

78   drivers of τ suggests that the results are unlikely to be solely determined by biases within the BioTIME

79   database, future work should seek to improve the scope and resolution of available data to enable more

80   strongly parametric analyses and examine additional measures of community change. While available trait

81   databases of amniotes and fish are carefully curated, checked and taxonomically tidy, the other databases

82   pose more problems in terms of taxonomic matching and consistency of trait measurements. Without direct

83   correspondence between dynamics and trait data sources, it is necessary to take traits as fixed values for each

84   species, despite known differences in traits in time[30–32] and space[33] that may themselves represent responses

85   to global change. However, in Celtic sea fish within-species shifts have been shown to contribute less to

86   community-level size shifts than changes in species composition [34]. We also note that 'size' traits for

87   indeterminately growing plants have a less clear meaning than for animals. However, both seed size and

88   maximum height are linked to environmental variables[35,36] and could therefore be hypothesised to influence

89   species responses to global change.

90   Many of the criticisms and defences regarding earlier studies using the BioTIME dataset, and indeed other

91   metanalyses of large collections of time series, also apply to this work[37]. The statistical approach was

92   developed to be as robust as possible to both incomplete trait data and changes in overall abundance and

93   sampling effort through time. However, it must be noted that our largely non-parametric approach could lack

94   the power and resolution to identify subtle changes. Biases in the underlying BioTIME database towards

95   vertebrate taxa and North American and European sites[14] are further exaggerated when crossed with trait

96   data availability (Figure 1b). One particularly concerning gap is the absence of any insect studies due to a

97   paucity of usable trait information. Observations suggest there have been considerable changes in the

98   structure of insect communities[24,38,39]. Developing comprehensive insect trait datasets, including using proxies

99   and data imputation, will be crucial to address this deficit[40–42].

100   In conclusion, despite these reservations, this global analysis suggests that cases of relative increases of larger

101   species[24,43] or trait constancy despite declines in abundance[44], may in fact be as frequent as shifts towards

102   smaller sized species[22]. Community responses may therefore be considerably more nuanced and localised than

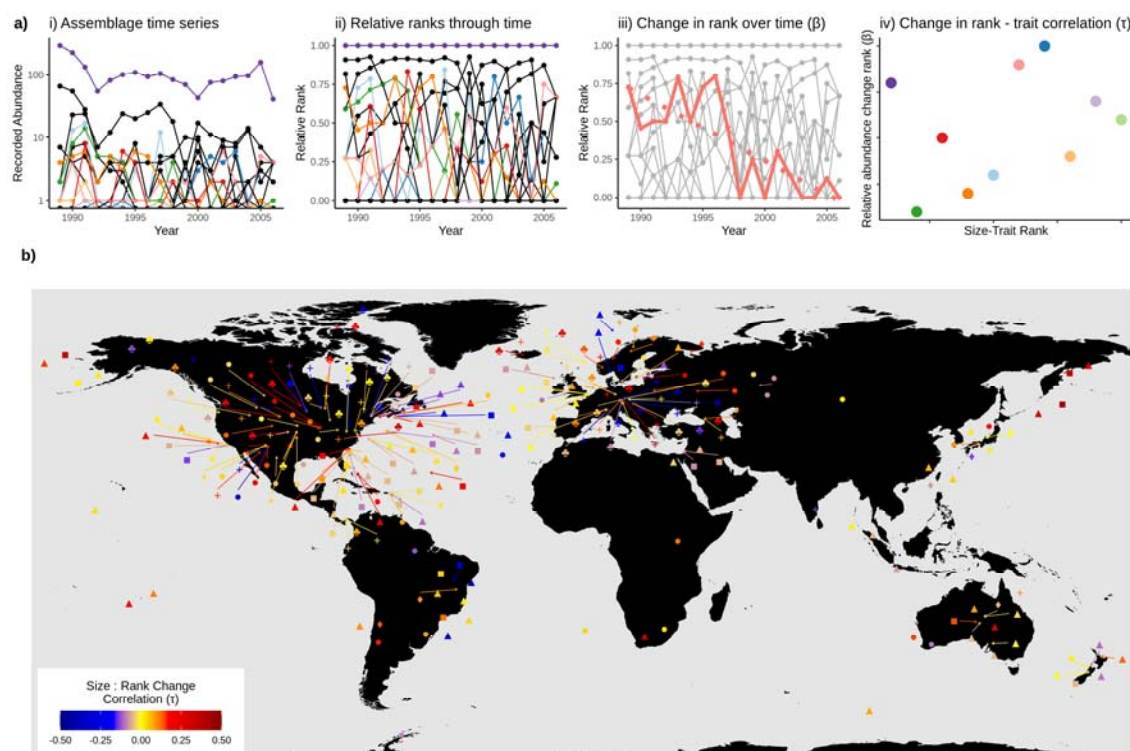103   previously considered based on macroecological expectations[8].

104
105 **Figure 1.** a) Example of the non-parametric approach taken to accomadate patchy trait data and possible

106 variation in sampling intensity through time for an arbitrary example assemblage. Here species with trait

107 values are coloured, others without trait data are black. (i) Quantitative survey data is combined to generate

108 assemblage time series. (ii) the relative ranks of each species are calculated for each year, through which is fit

109 a linear model summarising the rate of change (β) in a species rank through time (iii). For those species where

110 trait data is available, the concordance between body size traits and abundance rank changes (iv) is then

111 summarised by τ, the Kendal rank-correlation coefficient (here, $\tau = 0.24$). b) Global distribution of studies, for

112 each tested trait, showing average τ for each study-trait combination. Marine: Body length = ▲, Marine:

113 Qualitative body size = ■, Fish: Maximum length = ⬡, Amniotes: Adult body mass = ⬡, Plants: Seed mass = +,

114 Plants: Maximum height = ⬡. Note that the locations are shown as centre point of each study, which can cause

115 oceanic studies to be 'located' on land. See Extended Data Table 4 for full details of study-level results.
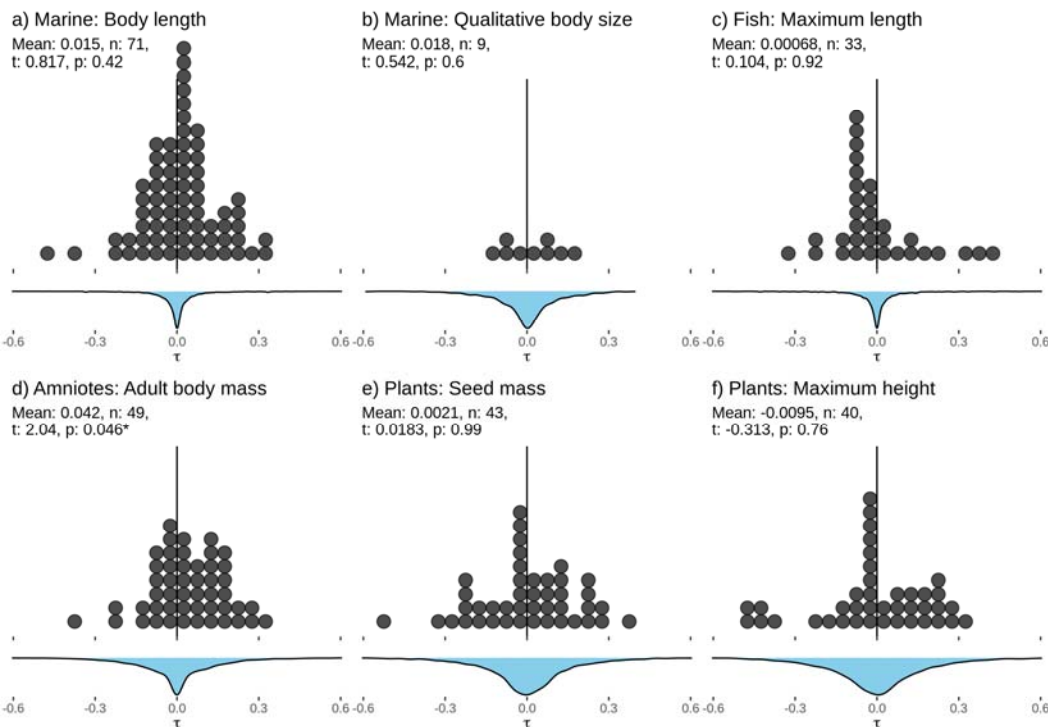
Figure 2. Distribution of Kendall's rank correlation coefficient between the 6 tested body-size traits and changes in relative abundance through time ('τ'). Each dot represents one study, averaging across the constituent assembly time series for studies of large spatial extent. Results are binned into classes 0.05 units of τ wide. Blue density plots show the distribution of 50 randomisations of available trait data. Statistical results refer to two-sided two-sample t-tests, comparing the distribution of observed τ values to the null distribution. Means shown are for the observed results. Full statistical results are given in Extended Data Table 1.

124 ## Methods

125 **Generating assemblage time series.** We downloaded all studies available in the 'open' component of the

126 BioTIME database of community time series[14] from https://doi.org/10.5281/zenodo.3265871. BioTIME

127 contains observations from both fixed plots (repeat measures from the same set of specific localised sites) and

128 from wide ranging surveys and transects that may not necessarily precisely align year-on-year. We followed

129 previous approaches[1] and first identified studies as 'multi-site' or 'single-site' based on the number of

130 coordinates in the BioTIME database. Single site studies were considered as one combined assemblage, while

131 widely-dispersed 'multi-site' studies were portioned into assemblages based on a global hexagonal grid of 96

132 km^2 cells using *dggridR*[45]. We retained records from assemblages with abundance or biomass data of at least

133 10 distinct species and at least 5 years between the first and the last record.

134 **Cleaning Names** Although the majority of the records are identified with binomials to species level, a portion

135 of the records in the BioTIME database are labelled only at higher taxonomic levels. For simplicity, we refer to

136 all distinct names as 'species'. We identified uninformative labels (for example 'spA', 'unidentified',

137 'Miscellaneous', 'larvae', 'grass') and common names (mostly birds) were converted to binomials using the

138 Encyclopaedia of Life tool via the *taxize* R package[46,47] followed by manual inspection based on study location

139 and species distribution where multiple options were presented. We excluded studies where the species are

140 listed using codes. Informative names were standardised against the GBIF name backbone[48] using *taxize*. The

141 dominant kingdom represented in each study was used to distinguish homonyms. Where BioTIME included

142 only a genus level identification, we matched these to genus level trait values listed in trait databases. Where

143 BioTIME only included taxonomic information of higher rank than genus, we did not attempt to match the

144 traits.

145 **Trait data** We used four separate trait databases that include some measure of organism size, but we did not

146 mix information between databases. *Amniotes*: The life history database was downloaded from

147 https://doi.org/10.6084/m9.figshare.c.3308127.v1[15] from which we used the 'adult_body_mass_g' field.

148 *Plants*: We downloaded from the TRY database (https://www.try-db.org/)[17] all records of 'seed dry mass' (trait

149 26) and 'plant height vegetative' (trait 3106). We grouped these by accepted species name, and calculated the

150 mean of the $\log 10$ (seedmass) values and the maximum observed height. We did not assign a value when the

151 standard deviation of $\log 10$ (seedmass) values was greater than 1. The resultant dataset was derived from 91

152 original datasets[51-123]. *Fish*: We downloaded a curated database of fish traits from

153 https://store.pangaea.de/Publications/Beukhof-etal_2019/TraitCollectionFishNAtlanticNEPacificContShelf.xlsx

154 [18] which in turn is largely based on data from the FishBase database[19]. It is focussed on the North Atlantic and

155 Pacific continental shelf, but this represents the majority of the relevant BioTIME studies. It includes values for

156 both genus and species level. We used maximum length, and when there were multiple values for a particular

157 species, we took an average. *Marine*: We downloaded size data from the World Register of Marine Species

158 (WoRMS) database[16]. Aphia IDs for all the species in our assemblages (excluding plants and fungi) were

159 identified and used to download all attributes associated with these IDs held on WoRMS using the *worrms* R

160 package[49]. Quantitative 'body size' measurements of length were scaled to millimetre units. We discarded

161   values from stages other than adults, values corresponding to minimums or thicknesses, then took a mean,

162   except where the values differed by over an order of magnitude, which we discarded. Qualitative body sizes

163   were divided into four categories (<0.2 mm , 0.2 - 2mm, 2-200 mm, >200 mm), that were carried forwards as

164   simple numbers (1-4). Data not from adults was discarded, and where an ID was associated with multiple

165   distinct size categories, it was discarded.

166   Summaries of the trait data completeness are given in Extended Data Figure 2. Note that 80 studies had

167   sufficient trait data for analysis under multiple traits - 36 had both categories of plant data, 31 had length data

168   from both WoRMS and the fish-specific database, 7 studies spanned the amniote life history traits and WoRMS

169   database, 5 studies shared both qualitative and quantitative size information from WoRMS, and one study

170   could be related to both traits from WoRMS and the fish database.

171   **Abundance change – trait correlation.** We assessed each assemblage-trait combination where ≥40% of the

172   species had data for that trait. Within each year, all n species in the assemblage were assigned relative ranks (1

173   = highest, 1/n = lowest) by their abundance or biomass depending on the fields available in BioTIME. Ties were

174   averaged and where a species was not observed in a particular year, it was assigned a rank of zero for that

175   year. Where a study included both 'abundance' and 'biomass' data, we preferentially used the abundance

176   data. Presence absence-data was not used. We fit a linear model through the relative ranks over time of each

177   species in the assemblage. The set of slopes (β) of these linear models within each dataset summarised the

178   relative change in abundance of each species in the assemblage through time. Very small β values, caused by

179   model fitting errors when there is no change in rank abundance, were set to 0 to avoid spurious rankings. The

180   main response variable 'τ' for each assemblage was then computed as Kendall's rank correlation coefficient

181   between trait values and the set of βs. Species with missing trait values were excluded. The default 'τ_B'

182   approach was used for ties[50]. Where there were multiple assemblages per study, study level τ was a simple

183   arithmetic mean of all assemblage level τ values.

184   **Statistics** To generate a null model for the impact of traits, the relative abundance rank changes (βs) were

185   computed as above, but the available trait values (including 'NA's where trait data was missing) were randomly

186   reassigned to the species in that assemblage and τ recalculated. This was repeated 100 times per assemblage

187   to generate a null distribution of expected τ values for each study. For each tested trait, we used two-sided

188   Welch's two-sample t-test to determine if the mean τ for that trait was significantly different to this null

189   expectation.

190   To examine study level determinates of τ within each trait, for each study we calculated: 1) the mean total

191   species richness of each assemblage over the time frame, 2) the mean assemblage level trait data

192   completeness, 3) the mean number of years that from which there was data, 4) the mean span of years from

193   which there was data, 5) the number of assemblages within the study (i.e. the spatial extent), 6) the grain size

194   of the study, as listed in the BioTIME metadata, and 7) the absolute latitude of the centre of the study. We fit a

195   set of linear models to assess whether these factors could predict either τ or τ^2.

203 Code Availability

204 All analyses were conducted using R. Code and illustrative notebooks to reproduce all steps is available at:

205 https://github.com/jcdterry/BioTIME_BodySize and archived on Zenodo at

206 https://doi.org/10.5281/zenodo.4745554

207 Data Availability

208 Original sources of open-source datasets are listed in the methods. Processed data are available with analysis

209 code at: https://github.com/jcdterry/BioTIME_BodySize and archived on Zenodo at

210 https://doi.org/10.5281/zenodo.4745554

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