



Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., & Genner, M. J. (2020). Climate change drives poleward increases and equatorward declines in marine species. *Current Biology*, 30 (8), 1572-1577.E2.  
<https://doi.org/10.1016/j.cub.2020.02.043>

Peer reviewed version

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[10.1016/j.cub.2020.02.043](https://doi.org/10.1016/j.cub.2020.02.043)

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1 **Climate change drives poleward increases**  
2 **and equatorward declines in marine species**

3

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14 **Summary**

15

16 Marine environments have increased in temperature by an average of 1°C since pre-industrial  
17 (1850) times [1]. Given that species ranges are closely allied to physiological thermal  
18 tolerances in marine organisms [2], it may therefore be expected that ocean warming would  
19 lead to abundance increases at poleward side of ranges, and abundance declines towards  
20 the equator [3]. Here we report a global analysis of abundance trends of 304 widely distributed  
21 marine species over the last century, across a range of taxonomic groups from phytoplankton  
22 to fish and marine mammals. Specifically, using a literature database we investigate the extent  
23 that the direction and strength of long-term species abundance changes depend on the  
24 sampled location within the latitudinal range of species. Our results show that abundance  
25 increases have been most prominent where sampling has taken place at the poleward side of  
26 species ranges, while abundance declines have been most prominent where sampling has  
27 taken place at the equatorward side of species ranges. These data provide evidence of  
28 omnipresent large-scale changes in abundance of marine species consistent with warming  
29 over the last century, and suggest that adaptation has not provided a buffer against the  
30 negative effects of warmer conditions at the equatorward extent of species ranges. On the  
31 basis of these results we suggest that projected sea temperature increases of up to 1.5°C  
32 over pre-industrial levels by 2050 [4] will continue to drive latitudinal abundance shifts in  
33 marine species, including those of importance for coastal livelihoods.

## 34 **Results and Discussion**

35

36 Marine organisms have a temperature range outside of which physiological processes cease  
37 to be optimal. As such, species distributions often correspond closely with physiological  
38 temperature limits [2, 5]. Cold tolerance can determine the position of the poleward edge of a  
39 species range, and consequently, ocean warming is expected to increase organismal  
40 performance, survival and reproductive success at higher latitudes of species ranges. It has  
41 therefore been predicted that warming seas should also drive increases in the abundance of  
42 species at their poleward range side [6]. Equally, warm tolerance is strongly associated with  
43 the position of the equatorward edge of marine species ranges. Hence, as oceans warm we  
44 may expect to find reductions in performance, survival and recruitment at lower latitudes of  
45 species ranges, leading to reductions in abundance at equatorward range limits [4].

46

47 Importantly, however, space use by marine species is not simply determined by thermal  
48 affinities. Species distributions and abundances are also dependent upon availability of core  
49 ecological resources such as food and substrate, which are not homogeneously distributed  
50 across species ranges. Consequently, distributions of species may not be fully predicted on  
51 the basis of the thermal environment and physiological tolerances alone [7]. Moreover, the  
52 temporal population-abundance response of species to warming at any position in their range  
53 may not exclusively depend on their thermal physiology, but also the responses of the species  
54 with which they interact [8]. An additional consideration is that regional temperature shifts are  
55 not the only physical changes in the marine environment associated with climate change, as  
56 parallel changes to storminess [9, 10], salinity [11], acidification [12] and sea ice conditions  
57 [13] have also been reported. To fully understand abundance changes of populations requires  
58 a comprehensive understanding of marine environmental change, as well as the physiological,  
59 life history and ecological characteristics of study species [14].

60

61 Despite the intrinsic complexities of marine biological systems, analyses from local and  
62 regional datasets suggest that thermal affinities are strong predictors of the responses of  
63 marine species to increasing temperatures [15, 16]. In general, studies have reported that  
64 within local communities warm-adapted species have increased in abundance, relative to  
65 cool-adapted species that have declined in abundance [2, 6, 15, 16]. However, such studies  
66 tend to be limited to a small number of species and a single locality or region. A more complete  
67 understanding of large-scale patterns of climate-associated local abundance change requires  
68 combining information from multiple studies across broad taxonomic diversity, and across  
69 wider spatial scales that encompass the full realised latitudinal distributions of study species  
70 [17]. In the most comprehensive analyses of marine species to date, abundance responses

71 have been interpreted as being at poleward and equatorward limits [2] or “consistent” or  
72 “inconsistent” with climate change [17] based on the findings of the original authors. However,  
73 a fully quantitative approach is required to test the strength of evidence for species-level  
74 poleward abundance increases and equatorward abundance declines within marine  
75 systems over the last century. Here, we consider abundance trends of marine species over  
76 the last century within an explicit latitudinal and quantitative framework.

77

78 We extracted all single-species abundance change observations from a published meta-  
79 database covering literature published from 1991 to 2012 [17], and added further records  
80 published from 2012 to 2016. For each record we ensured the direction of abundance change  
81 during the study was recorded (either positive or negative, with respect to time or  
82 temperature), and ensured each record had an accompanying survey location (Figure 1A).  
83 We then identified the relative latitudinal position of the survey location within the known  
84 latitudinal distribution of the species, as determined from occurrence data within the Global  
85 Biodiversity Information Facility (GBIF) database [18]. In total the complete dataset included  
86 540 records of abundance change, across 304 species (average 1.67 records per species;  
87 range 1 to 21) ranging from phytoplankton and macroalgae, to seabirds and marine mammals  
88 (Figure 1B). We then used these data to generate linear models that examined how the  
89 direction of abundance change was dependent on the latitudinal position of the survey, and if  
90 there were any biases in responses associated with hemisphere of study or the survey  
91 methods (i.e. time-span of study, and whether the study was a continuous time series, an  
92 irregularly sampled study, or a two-point comparison).

93

94 Analyses based on our complete dataset of 540 sets of records demonstrated that the location  
95 of sampling within the species range was a highly significant predictor of the direction of  
96 abundance change (Table S1). Specifically, marine species were significantly more likely to  
97 have increased in abundance if a study had been undertaken at the poleward range side than  
98 at the equatorward range side. By contrast species were significantly more likely to have  
99 declined in abundance if a study had been undertaken at the equatorward side than the  
100 poleward range side (Figure 2A). We found no influence of survey methods or hemisphere of  
101 the study (Table S1). We repeated analyses on a subset of the dataset where the original  
102 authors report a statistically significant change in abundance over the study period (185 from  
103 540 records), and again we found the position in the latitudinal range of the species to be the  
104 most important predictor of the direction of abundance change (Figure 2B). Next, we explored  
105 the strength of abundance responses to temperature (or year) using the reported correlation  
106 coefficients ( $r$  values) that were available for 77 from 540 records. Again, we found greater

107 negative responses occurring at the equatorial range margins and more positive responses at  
108 the polar side of species distributions (Figure 2C).

109

110 Our study relies on published abundance trends being unbiased representations of  
111 abundance changes in the natural environment. However, there is a possibility that  
112 observations of significant abundance change matching expectations from climate change are  
113 more likely to be selected for publication [19]. This effect is plausibly strongest in single-  
114 species studies [17], which comprised 68 records in our analysis, so we repeated analyses on  
115 only the 472 records from multispecies studies. Our analyses were robust with respect to  
116 potential publication bias, with position of the study within the latitudinal range again the  
117 strongest predictor of the direction of abundance responses in the multispecies analysis (Table  
118 S1). The reported observations in our dataset are spatially clustered, with the majority of  
119 observations (448 of the 540 records) from the Northern Hemisphere, and were concentrated  
120 in the temperate continental shelf waters of Europe, North America and Japan (Figure 1A). To  
121 investigate potential influence of spatial bias we subsampled the data to exclude records that  
122 were in close spatial proximity to other records from the same species (within the same 1  
123 degree latitude × longitude grid cell). The analysis of this spatially thinned dataset (478 of the  
124 540 records) again resolved latitudinal position of the study within the range of the species as  
125 the most reliable predictor of the direction of abundance change. Taken together these  
126 analyses indicate the data are robust to publication and spatial biases, however further work  
127 is required across undersampled regions and taxonomic or functional groups to fully  
128 understand the global extent of the observed pattern.

129

130 Addressing taxonomic bias, we explored if survey position in the species range was a  
131 consistent predictor of species responses among each of the five taxonomic or functional  
132 groups that were most well represented in the dataset, namely non-larval fishes, larval bony  
133 fishes, seabirds, benthic invertebrates, and zooplankton (Figure 1B). Although we found that  
134 the extent of the response varied significantly among these groups (Table S2), we found a  
135 consistent pattern of observed abundance increases at the poleward side of species range,  
136 and decline at equatorward sides in all taxonomic groups. This pattern was statistically  
137 significant in individual analyses of non-larval fishes, larval bony fishes and seabirds ( $P < 0.05$ ,  
138 Table S2), with larval bony fishes having a more pronounced positive response at the  
139 poleward side of their range relative to other groups (Table S2, Figure 3). This result highlights  
140 variation among marine organisms (and potentially their varied life stages) in their responses  
141 to warming. Differences among taxonomic or functional groups may be expected due to  
142 variation in life history traits including reproductive rates, dispersal biology, migratory

143 behaviour and growth rates [14], which in turn affect opportunities to maximise on ecological  
144 opportunity.

145

146 Clearly not all species and populations followed the general pattern, and such contrasts in  
147 responses to warming may be predicted in situations where thermal constraints are not  
148 necessarily the primary determinant of species ranges. Such situations can arise when the  
149 other physiological (e.g. oxygen availability) or ecological (e.g. food availability) constraints  
150 dominate, although such constraints often covary with temperature (e.g. [20]). Equally, there  
151 are situations where the latitudinal limit of a species is determined by a geographic barrier  
152 such as the presence of a continental landmass, or the absence of suitable substrate to  
153 colonise [21], rather than the thermal environment. Finally, the abundance of many species  
154 will also have been influenced by human activities in recent history, such as habitat  
155 degradation and fisheries, which may have already influenced population sizes and limited  
156 capacity for rapid response to climate warming [22].

157

158 We focused on latitudinal range limits of species, making the broad assumption that latitudinal  
159 gradients correspond with the thermal gradients that species occupy. However, while global  
160 thermal gradients are broadly colder towards the poles, a range of factors influence local  
161 temperature variation across latitude, depth and time. For example, surface ocean currents  
162 and upwelling can drive variation in associations between latitude and temperature [23].  
163 Equally, the pace of climate change is not homogeneous and can be inconsistent with  
164 latitudinal gradients [21, 24]. Although we found an overall association between time and  
165 temperature across all survey locations in this dataset, it is possible that abundance changes  
166 are more likely to be detected where the pace of climate change has been most rapid [25].

167

168 A notable result of this study was that populations at both polar and equatorial range margins  
169 are undergoing abundance changes. This is consistent with expectations that marine species  
170 have shifted abundance in line with their full thermal tolerance limits [2], and is important  
171 because it is suggestive of thermal tolerance limits of species being relatively inflexible over  
172 decadal timescales. Specifically, it also indicates that populations of marine organisms at the  
173 equatorial sides of species ranges are unable to adapt at a sufficiently rapid pace to enable  
174 them to thrive in warmer conditions. Evolutionary adaptation to warming conditions may be  
175 particularly slow for species with relatively long generation times such as the marine fishes  
176 [26] which dominate our dataset, but by contrast evolutionary adaptation may be expected to  
177 be more rapid in taxonomic or functional groups with fast life histories such as phytoplankton  
178 [27]. It is also plausible that differential responses of marine species to warming will result in

179 abundance shift mismatches between interdependent components of marine communities, for  
180 example predators and their prey [28].

181

182 We included a wide breadth of studies from across the globe, but ideally more records would  
183 be available from under-represented taxonomic or functional groups, including those of  
184 ecological and commercial importance. Additionally, the available data was strongly biased  
185 towards temperate latitudes and further work is needed to determine whether the same  
186 patterns hold for tropical species. With increased recognition of the value of long-term and  
187 resurvey data, increasing numbers of datasets are becoming available through initiatives to  
188 study broader patterns of biodiversity change [29, 30]. There are also efforts to bring together  
189 and standardise existing datasets over space and time, to enable abundance change  
190 estimates to be made across vast expanses of marine habitat [31]. Thus, it is possible that  
191 future analyses will be able to evaluate temporal abundance changes across much larger  
192 proportions of species ranges than are considered here, enabling a more thorough evaluation  
193 of how physiological, ecological, and life history traits interact with environmental variation to  
194 drive abundance changes within individual species.

195

196 In conclusion, the analyses presented here clearly demonstrate a pattern of local abundance  
197 change that is widespread in marine systems, most likely due to the combination of  
198 physiologically-determined thermal niches and changes in climatic variables. Thus, our study  
199 builds on evidence of climate-associated local abundance changes and sits alongside climate-  
200 driven changes in other biological parameters such as the overall distributions of species, and  
201 shifts in the timing of life history events [2]. Average sea surface temperatures are set to rise  
202 further over the course of this century [4] and the frequency of marine heatwaves is increasing  
203 [32]. It therefore seems plausible that local abundance changes linked to physiological and  
204 ecological tolerances will continue to take place at both the poleward and equatorward sides  
205 of species ranges impacting further on local marine assemblages and the coastal industries  
206 that depend on them.

207

## 208 **Acknowledgements**

209 The work was supported by NERC studentships NE/L501669/1 (to LAR) and NE/L002434/1  
210 (to JJF), with additional support for the literature survey from the UK Government Office for  
211 Science. RAC was supported through the NERC SeaDNA project NE/F001878/1.

212

## 213 **Author Contributions**

214 Conceptualization, M.J.G.; Data compilation, L.A.R., J.J.F. and R.A.H.; Methodology, R.A.H.,  
215 L.A.R., R.A.C and M.J.G.; Formal analysis, R.A.H., L.A.R., R.A.C and M.J.G.; Writing -



216 Original Draft, L.A.R., R.A.H. and M.J.G.; Writing - Review & Editing, L.A.R., J.J.F., R.A.C.,  
217 S.D.S., M.J.G.; Funding Acquisition, M.J.G. and S.D.S.

218

### 219 **Declaration of Interests**

220 The authors declare no competing interests.

221

### 222 **Main text figure/table legends**

223

#### 224 **Figure 1 – Spatial and taxonomic coverage of studies analysed.**

225 **A)** Global distribution of long-term abundance observations used in this analysis. **B)** Number  
226 of temporal abundance records analysed in each of the nine taxonomic or functional groups  
227 (total n=540). Map relief data from the ETOPO1 Global Relief Model [41]. Photos represent  
228 species in the dataset undertaking responses at range margins consistent with ocean  
229 warming: sea sparkle (*Noctiluca scintillans*) by M.A. Sampayo; common dolphin (*Delphinus*  
230 *delphis*) original source anonymous; Australasian gannet (*Morus serrator*) by J.J. Harrison;  
231 lined chiton (*Tonicella lineata*) by M. Knoth; Atlantic salmon (*Salmo salar*) by H.-P. Fjeld.  
232 Photos from Wikimedia commons licensed under the Creative Commons Attribution licences  
233 2.0 (chiton), 2.5 (salmon) or 3.0 (sea sparkle, dolphin, gannet).

234

#### 235 **Figure 2. Long-term abundance changes depend on the position of sampling stations** 236 **within the latitudinal range of species.**

237 **A)** Abundance changes across all 540 records. **B)** Abundance changes recorded as significant  
238 in original data sources, 185 records in total. **C)** Reported *r* values for abundance change over  
239 time or temperature in original data sources, 77 records in total. The blue shaded area  
240 indicates the 95% confidence interval, while vertical lines represent datapoints that reflect  
241 either positive (1 in binomial model, shown as +1 on axis), or negative abundance changes (0  
242 in binomial model, shown as -1 on axis). See Table S1 for full model details.

243

#### 244 **Figure 3. Associations between relative position in latitudinal range and direction of** 245 **the abundance change within each taxonomic/functional group.**

246 Abundance changes over the study time periods for A) Fish, B) Larval bony fish, C)  
247 Invertebrates (other), D) Seabirds, E) Zooplankton. These species groups represent the five  
248 most well represented groups within the main dataset. The blue shaded area indicates the  
249 95% confidence interval, while vertical lines represent datapoints that were either positive (1  
250 in binomial model, shown as +1 on axis), or negative (0 in model, shown as -1 on axis). See  
251 Table S2 for full model details.

252

253 **STAR★Methods**

254

255 **Lead Contact and Materials Availability**

256 Further information and requests for resources should be directed to and will be fulfilled by the  
257 Lead Contact, Martin Genner ([M.Genner@bristol.ac.uk](mailto:M.Genner@bristol.ac.uk)). This study did not generate new  
258 unique reagents.

259

260 **Method Details**

261 We sourced data on the abundance changes of marine species from two sources. First, we  
262 used the database generated by Poloczanska, et al. [17] that covered literature published  
263 between 1991 to 2012, and we extracted the records where abundance was the response  
264 variable. We then checked original papers to ensure observations were from fully marine  
265 species or species dependent on the ocean, and then also checked and assigned direction of  
266 the abundance response over the studied time interval. Secondly, we compiled observations  
267 from literature published between 2012 and 2016 using the same methodology as  
268 Poloczanska et al. [17]. For both sets of records we retained only those where abundance  
269 trends could clearly be attributed to individual species. Each study was defined as a  
270 continuous time series, an irregularly sampled study or a two-point comparison, as determined  
271 from the original paper. Studies were categorised as single-species (reporting trends for one  
272 species only) or multispecies (abundance trends for multiple species reported).

273

274 We included cases where abundance changes were correlated against time and cases  
275 where abundance changes were correlated against temperature. We quantified the  
276 association between time and temperature at study locations using the correlation coefficient  
277 ( $r$ ) between year and mean annual sea surface temperature (SST). Mean annual SST was  
278 obtained for each latitude and longitude cell from monthly HadISST data, across every year  
279 of a study period [39]. This was performed for 139 of 157 unique locations, based on  
280 availability of consistent mean annual temperature data for the full study period. Overall,  
281 temperature and time were positively correlated in the locations and durations of the original  
282 studies, with an average correlation coefficient  $r = 0.34$ .

283

284 To assign positive or negative abundance trends for species at their study location, we used  
285 a three-step sequential process. First, and preferentially, where a study reported a  
286 statistically-significant abundance change, we used those records. Second, where significant  
287 responses were not recorded, but the direction of change was quantitatively described in the  
288 text, then those records were used. Third, where no quantitative assessment was provided  
289 in the text, but a visual image of the abundance data was available, we determined the trend

290 from the plotted data. In cases where abundance responses to both temperature and time  
291 were recorded, only the association with temperature analysis was included in analyses.  
292 Where the environmental variable reported was not explicitly temperature or time (e.g. sea  
293 ice), we ensured that the environmental variable was clearly associated with temperature or  
294 time by the original authors.

295

296 Occurrence data for each species were obtained from GBIF [18] via the ModestR tool [33]. A  
297 taxonomy for each species, from species to class rank is required for ModestR, and this was  
298 constructed using taxonomic information from the World Register of Marine Species (WoRMS)  
299 [38]. Any species that had been re-classified since the publication of the paper that the  
300 observation originated from were renamed in line with the accepted WoRMS taxonomy.  
301 ModestR was used to collate, visualise and check species occurrences from GBIF and to  
302 export the geographical coordinates associated with these records as text files (one file per  
303 species). We excluded 0,0 coordinates, occurrences falling on land, and duplicate coordinates  
304 to two decimal places. Where studies were conducted outside the recognised GBIF range  
305 they were assigned 1 for more poleward and 0 for closer to the equator to reflect the extreme  
306 range edge of the particular survey location.

307

308 Some species had occurrence records in both the northern and southern hemispheres. If the  
309 original survey location for a species in the database was undertaken in the Northern  
310 Hemisphere, we deleted from the dataset all coordinates from the Southern Hemisphere for  
311 that species, and vice versa. Species that were the focus of studies in both hemispheres were  
312 treated as two discrete entities, for example being referred to as "*Species name N*" and  
313 "*Species name S*". To avoid erroneous points or outliers having an undue influence on the  
314 species ranges, we removed 2% of the most extreme latitudinal records, 1% from each side  
315 of the range. We then checked resultant records visually for any remaining outliers, which  
316 were then deleted. To ensure latitudinal ranges were well characterised and reliable, any  
317 species left with fewer than 50 observations were excluded from further analysis. After these  
318 checks and deletions, we retained 540 abundance trend records from 304 species. Of these  
319 540 trend records 185 were reported as significant in the original studies, and we generated  
320 a subset comprising only these significant record for some analyses due to the potential for  
321 non-significant trends to introduce type II errors in results.

322

323 To generate a spatially-thinned subset, we subsampled the 540 abundance trend records by  
324 removing repeat data for the same species within each 1° latitude and longitude grid cell. The  
325 dataset was first sorted by species and grid cell, and where two or more records of abundance  
326 change were reported the longest time series was retained (if records covered the same time

327 period, we systematically removed the first record in the data list). In total 62 records were  
328 removed from the full dataset to generate this spatially thinned subset of the data.

329

### 330 **Quantification and Statistical Analysis**

331 We calculated the relative latitudinal position of each study sampling location within the range  
332 of the focal species using the formula:

333

$$334 \quad \text{Sampling position} \in \text{species range} = \frac{\text{study latitude} - \text{equatorward extreme}}{\text{poleward extreme} - \text{equatorward extreme}}$$

335

336 Where equatorward and poleward extremes were identified from the cleaned GBIF records,  
337 we modelled the association between the direction of the abundance change and predictor  
338 variables using Generalized Linear Mixed-Effects Model (GLMER-Model 1) with a binomial  
339 response with a link logit using the lme4 package in R 3.6.0 [34, 40]. We used these models  
340 to analyse several data subsets including: the full dataset, only records with significant trends,  
341 only multispecies studies and spatially thinned data. In these models fixed effects included:  
342 sampling position in species range, study hemisphere, study timespan, and study type  
343 (continuous time series, irregular or two-point). Random effects included: taxonomic group  
344 (fishes, benthic invertebrates, larval fishes, macroalgae, mammals/reptiles, phytoplankton,  
345 seabirds, seagrass, zooplankton) and study (as multiple observations were typically reported  
346 in individual studies). Generalised linear models (GLM-Model 2) were subsequently used to  
347 generate simpler models with sampling position in species range as the sole predictor variable.

348

349 We modelled the association between reported  $r$ -values (including square-root transformed  $r^2$   
350 values) and the same set of predictor variables reported above using linear mixed-effects  
351 models (Model 3). We then used linear models (Model 4) with sampling position in species  
352 range as the sole predictor variable. The lmerTest package was used to extract output from  
353 mixed models. Model outputs were plotted using the effects package [36] (Fig. 2).  $R^2$  values  
354 were obtained using the r2glmm package [35].

355

### 356 **Data and Code Availability**

357 *All datasets and code are available at <https://doi.org/10.6084/m9.figshare.11848152>*

358

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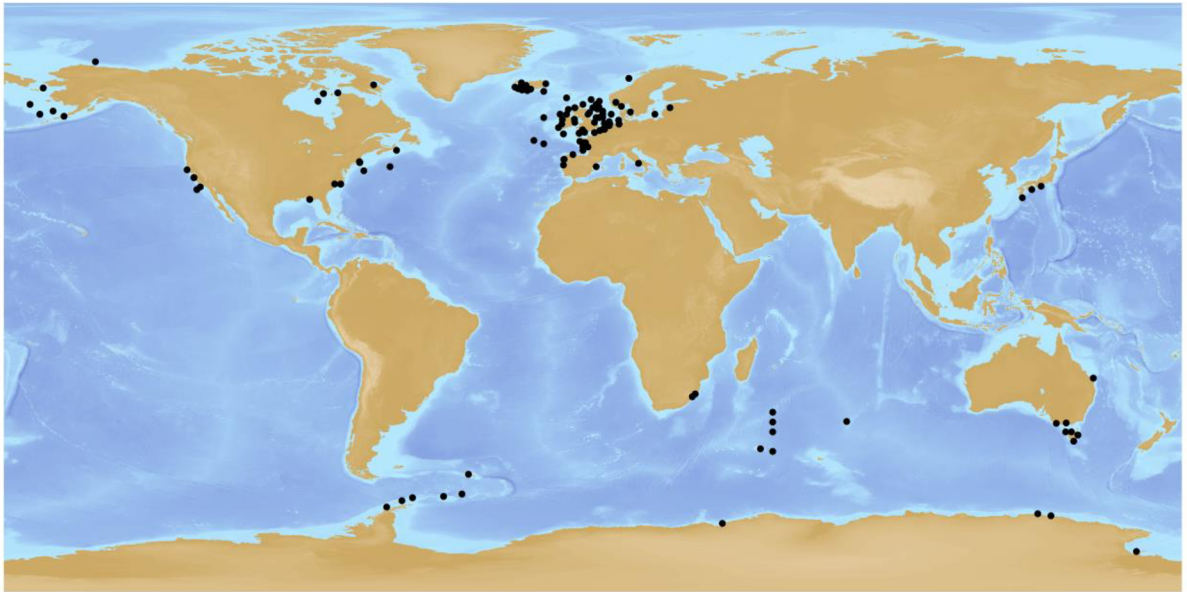
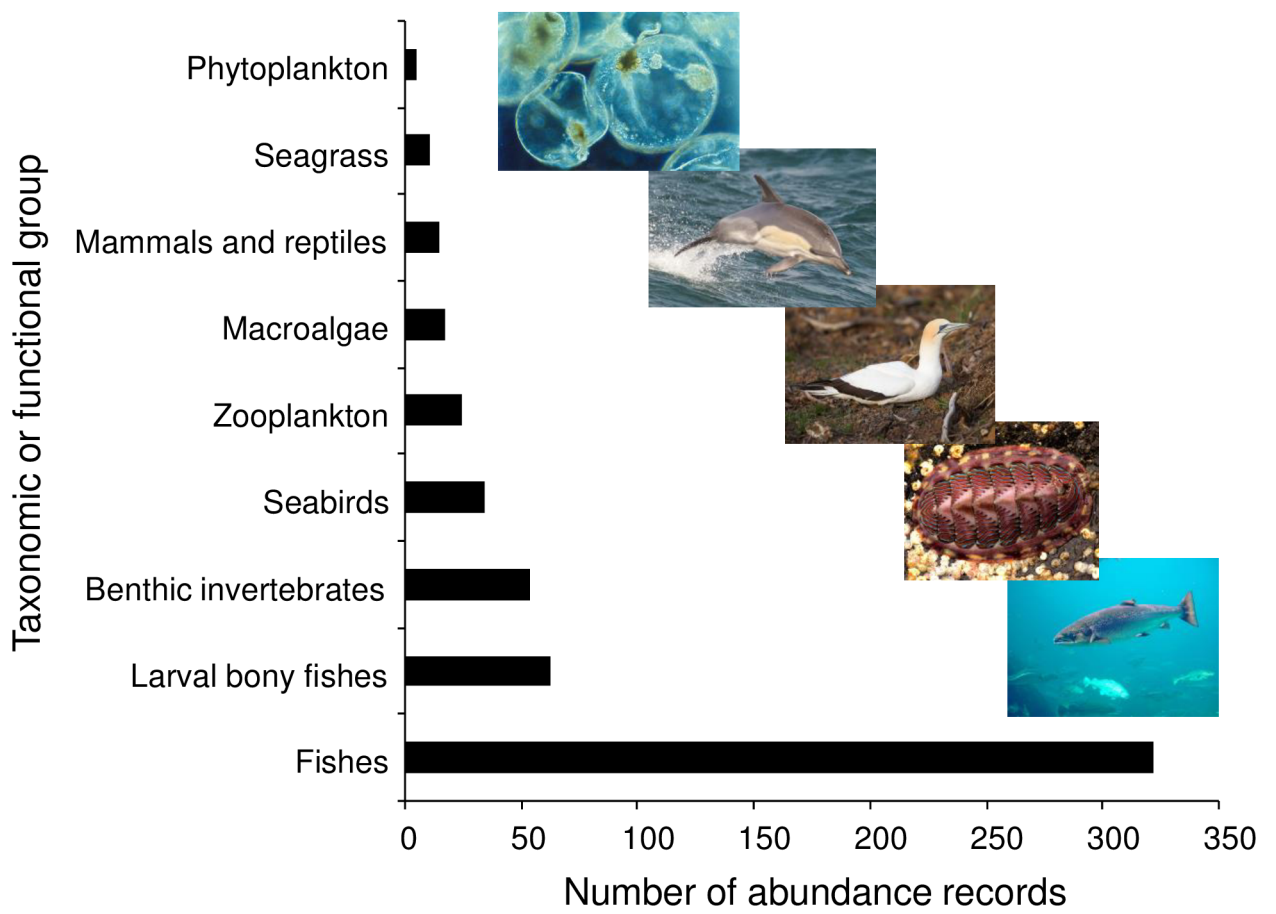
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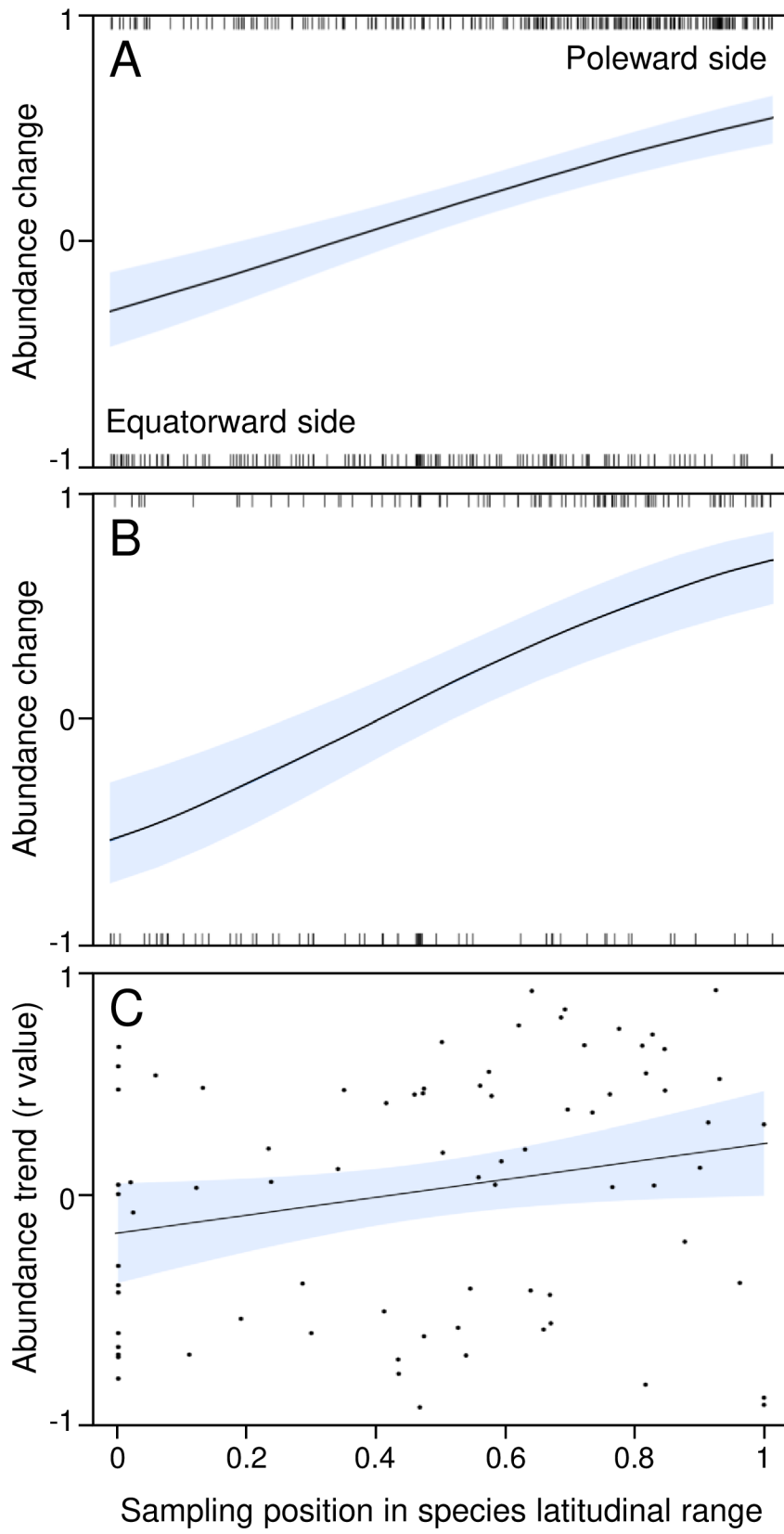
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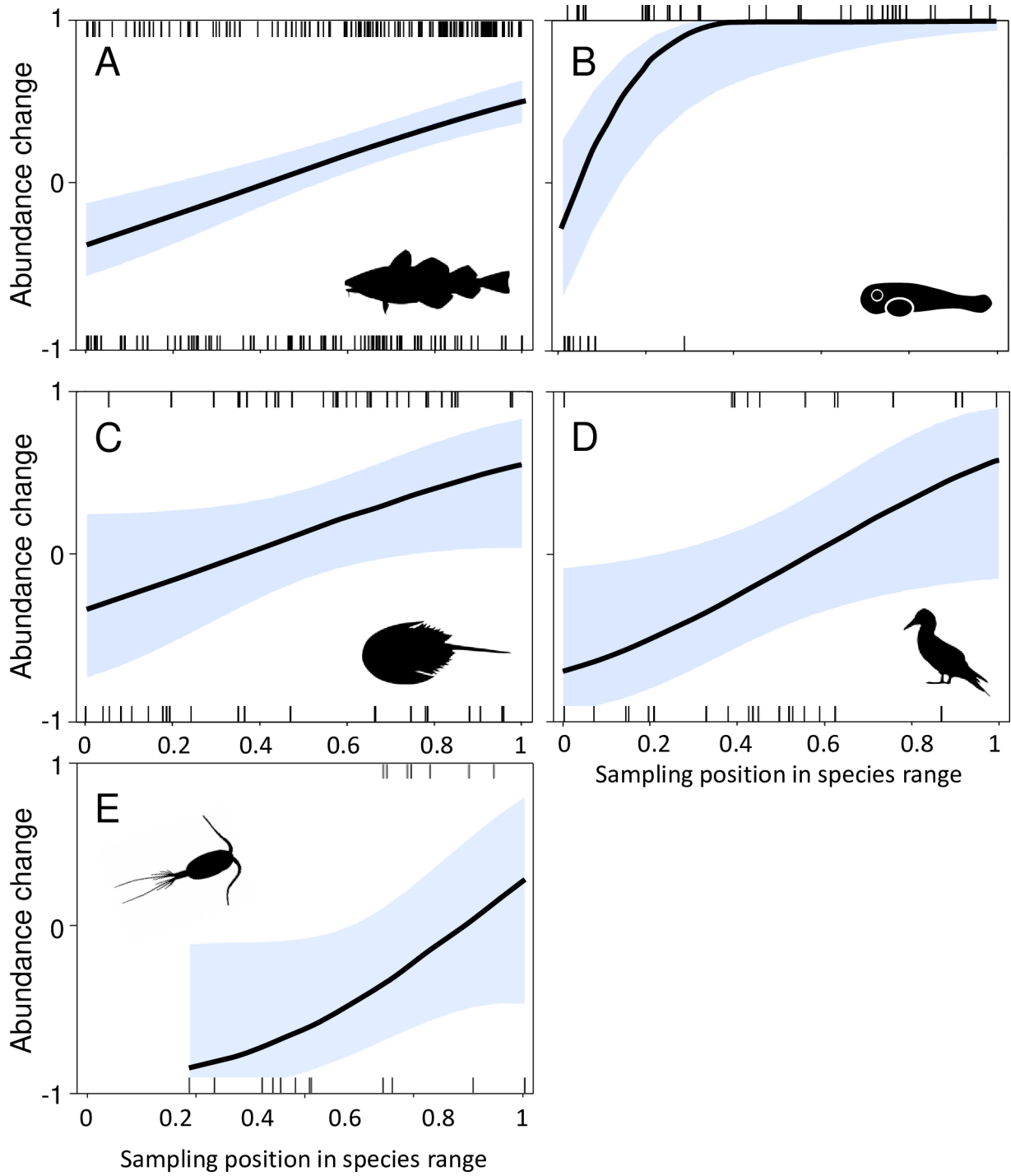
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**A****B**





## Key Resources Table

RESOURCE	SOURCE	IDENTIFIER
<b>Deposited Data</b>		
Data analysed and analysis code	This paper	<a href="https://doi.org/10.6084/m9.figshare.11848152">https://doi.org/10.6084/m9.figshare.11848152</a>
<b>Software and Algorithms</b>		
R	R Core team	<a href="https://www.r-project.org/">https://www.r-project.org/</a>
ModestR	[33]	<a href="http://www.ipez.es/ModestR/">http://www.ipez.es/ModestR/</a>
lme4 package	[34]	<a href="https://github.com/lme4/lme4/">https://github.com/lme4/lme4/</a>
r2glmm package	[35]	<a href="https://www.rdocumentation.org/packages/r2glmm">https://www.rdocumentation.org/packages/r2glmm</a>
effects package	[36]	<a href="https://www.rdocumentation.org/packages/effects/versions/4.1-3/topics/effects-package">https://www.rdocumentation.org/packages/effects/versions/4.1-3/topics/effects-package</a>
lmerTest package	[37]	<a href="https://www.rdocumentation.org/packages/lmerTest/versions/3.1-1">https://www.rdocumentation.org/packages/lmerTest/versions/3.1-1</a>
glm	R Core team	<a href="https://www.r-project.org/">https://www.r-project.org/</a>
<b>Other</b>		
Referenced dataset	[17]	<a href="https://doi.org/10.1038/nclimate1958">doi.org/10.1038/nclimate1958</a>
GBIF	[18]	<a href="https://www.gbif.org/">https://www.gbif.org/</a>
WoRMS	[38]	<a href="http://marinespecies.org/">http://marinespecies.org/</a>
HADISST	[39]	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/">www.metoffice.gov.uk/hadobs/hadisst/</a>

## Full dataset analysis

	Estimate	Std. Error	z value	P	r <sup>2</sup>
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.169	0.638	-1.833	0.067	-
Position (in species range)	2.665	0.406	6.57	<0.001	0.088
Timespan (of study)	0.002	0.007	0.347	0.728	0.000
Sampling (type timeseries)	-0.261	0.416	-0.626	0.532	0.001
Sampling (type twopoint)	-1.717	1.121	-1.531	0.126	0.004
Hemisphere	0.59	0.512	1.151	0.250	0.006
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))					
(Intercept)	-0.6381	0.1865	-3.421	0.001	-
Position (in species range)	1.8748	0.2858	6.561	<0.001	0.075

## Records with statistically significant abundance shifts only

	Estimate	Std. Error	z value	P	r <sup>2</sup>
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.99735	1.190	-1.678	0.093	-
Position (in species range)	3.70236	0.713	5.194	<0.001	0.153
Timespan (of study)	0.01215	0.017	0.735	0.462	0.004
Sampling (type timeseries)	-0.30405	0.804	-0.378	0.705	0.002
Sampling (type twopoint)	-1.86467	1.424	-1.31	0.190	0.012
Hemisphere	0.50667	0.998	0.508	0.612	0.003
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"), data=dat)					
(Intercept)	-1.1933	0.3193	-3.738	0.000	-
Position (in species range)	2.9493	0.5479	5.383	0.000	0.14

## Multispecies studies only

	Estimate	Std. Error	z value	P	r <sup>2</sup>
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.101763	0.751	-1.467	0.143	-
Position (in species range)	2.513356	0.420	5.988	<0.001	0.087
Timespan (of study)	0.001139	0.008	0.142	0.887	0.000
Sampling (type timeseries)	-0.094943	0.471	-0.202	0.840	0.000
Sampling (type twopoint)	-1.863263	1.120	-1.663	0.096	0.006
Hemisphere	0.759877	0.580	1.31	0.190	0.010
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))					
(Intercept)	-0.4646	0.1965	-2.365	0.018	-
Position (in species range)	1.727	0.2985	5.785	0.000	0.650

## Spatially-thinned records

	Estimate	Std. Error	z value	P	r <sup>2</sup>
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.173461	0.63802	-1.839	6.59E-02	-
Position (in species range)	2.661017	0.405128	6.568	5.09E-11	0.960
Timespan (of study)	0.002592	0.007177	0.361	0.718	0.001
Sampling (type timeseries)	-0.252619	0.41595	-0.607	0.5436	0.001
Sampling (type twopoint)	-1.720151	1.120568	-1.535	0.1248	0.011
Hemisphere	0.585845	0.511921	1.144	0.2525	0.007

Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))

(Intercept)	-0.6824	0.2033	-3.357	0.001	-
Position (in species range)	1.8748	0.2858	6.561	<0.001	0.075

## Records with r values reported

	Estimate	Std. Error	df	t	P	r <sup>2</sup>
Model 3: lmer(r ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record))						
(Intercept)	-0.111502	0.588	18.397889	-0.190	0.852	-
Position (in species range)	0.437045	0.156	61.224134	2.808	0.007	0.062
Timespan (of study)	-0.002105	0.006	21.001368	-0.336	0.740	0.002
Sampling (type timeseries)	-0.168088	0.414	18.68575	-0.406	0.689	0.003
Sampling (type twopoint)	-0.11274	0.650	13.713493	-0.174	0.865	0.001
Position (in species range)	-0.414449	0.607	17.763703	-0.682	0.504	0.008

	Estimate	Std. Error	t	P	r <sup>2</sup>
Model 4: lm(r ~ Position)					
(Intercept)	-0.1526	0.1039	-1.468	0.146	-
Position (in species range)	0.3738	0.1795	2.083	0.041	0.055

## Table S1: Summary of model fixed effects, related to Figure 2.

Generalized Linear Mixed-Effects Model (Model 1) for association between the response variable (direction of the abundance change) and predictor variables and generalised linear model results for the reduced model (Model 2). A linear mixed-effect model was used for r value analysis as the values were continuous (Model 3) and a linear model for the reduced model (Model 4).

## Position\*Group

	Estimate	Std. Error	z value	P	r <sup>2</sup>
AbundanceChangeN ~ Position* taxa_gp, family=binomial("logit")					
(Intercept)	-0.73505	0.26062	-2.82	0.0048	-
Position (in species range)	1.88364	0.36516	5.158	2.49E-07	0.013
taxa_gp Invertebrates	0.07137	0.66351	0.108	0.9143	0.000
taxa_gp Larval fish	0.0791	0.65053	0.122	0.9032	0.007
taxa_gp Seabirds	-0.96201	0.83925	-1.146	0.2517	0.000
taxa_gp Zooplankton	-2.52858	1.6025	-1.578	0.1146	0.010
Position * taxa_gp Invertebrates	0.04586	1.11113	0.041	0.9671	0.000
Position * taxa_gp Larval fish	11.13908	4.94277	2.254	0.0242	0.221
Position * taxa_gp Seabirds	1.16963	1.48568	0.787	0.4311	0.000
Position * taxa_gp Zooplankton	1.98631	2.19916	0.903	0.3664	0.005

### Group-specific models

glm(Abundance Change~ Position, family = binomial("logit"))

	Estimate	Std. Error	z value	P	r <sup>2</sup>
<b>Zooplankton</b>					
(Intercept)	-3.264	1.581	-2.064	0.039	-
Position (in species range)	3.870	2.169	1.785	0.074	0.316
<b>Seabirds</b>					
(Intercept)	-1.697	0.798	-2.127	0.033	-
Position (in species range)	3.053	1.440	2.120	0.034	0.118
<b>Benthic Invertebrates</b>					
(Intercept)	-0.664	0.610	-1.088	0.277	-
Position (in species range)	1.930	1.049	1.839	0.066	0.052
<b>Fish</b>					
(Intercept)	-0.735	0.261	-2.820	0.005	-
Position (in species range)	1.884	0.365	5.158	<0.001	0.079
<b>Larval bony fish</b>					
(Intercept)	-0.656	0.596	-1.100	0.271	-
Position (in species range)	13.023	4.931	2.641	0.008	0.335

**Table S2. Summary of model fixed effects, related to Figure 3.**

Generalized linear models for testing for dependence of the response variable (direction of the abundance change) on both the position in range and taxonomic/functional group. The analysis included only the five most well represented groups within the main dataset.