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Prediction of unprecedented biological shifts in the global ocean

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29 Abstract

Impermanence is an ecological principle¹ but there are times when changes occur non-linearly as 30 31 Abrupt Community Shifts (ACSs) that transform the ecosystem state and the goods and services it 32 provides². Here, we present an ecological theory that can be used to explain and predict long-term 33 biological changes including ACSs at the global scale. We test our theory using 14 marine pelagic 34 ecosystems in tropical, temperate and polar regions using multi-decadal time series of marine 35 metazoans from zooplankton to fish. Predicted and observed long-term fluctuations correspond remarkably, including ACSs at the end of the 1980s³⁻⁶ and 1990s^{4,7}. Our analyses show that the shifts 36 37 result from changes in global temperature and/or large-scale atmospheric circulation that alter local 38 thermal regimes, which in turn interact with the thermal niche of species to trigger long-term and 39 sometimes abrupt shifts at the community level. Applying our theory to reconstruct ACSs at a global 40 spatial scale for the period 1960-2015 predicts the occurrence of a major ACS after 2014 that is unprecedented in magnitude (~3 times the average) and spatial extent, being ~5 times the average 41 42 and extending over ~14% of the oceans. The predicted ACS coincided with a super El Niño event as 43 well as major shifts in atmospheric circulation and temperature in the extratropical regions of the 44 Northern Hemisphere, and including the Arctic Ocean. Our results underline the sensitivity of the Arctic Ocean, an area that is currently experiencing an unprecedented melting that may lead to a complete 45 biological reorganisation of ecosystems^{4,8}. Finally, the application of our theory indicates the potential 46 47 for an increase in the size of such events in the future as the world warms in response to global climate 48 change.

49

50 Main text

51 After decades of research on the origin of long-term changes in biological communities and Abrupt 52 Community Shifts (ACSs), processes that drive those phenomena remain poorly understood^{3,7,9-13}.

Here, we define an ACS as a stepwise shift in community structure¹⁴, a definition that does not 53 necessarily implicate the existence of stable states^{2,12} that are rarely observed in the pelagic 54 environment¹³⁻¹⁵; they essentially indicate rapid and major alterations in species composition that may 55 56 significantly affect biodiversity with potential consequences for ecosystem services. A well-known 57 example is the ACS that developed across the North Pacific in the 1970s¹⁶. In this work, we used the MacroEcological Theory on the Arrangement of Life (METAL; Methods; see Supplementary Table 1 for 58 a list of the acronyms)^{14,17-19} to investigate long-term community changes in marine metazoans 59 (including ACSs) in the global ocean during the period 1960-2015. In each geographical cell of a gridded 60 ocean, we built pseudo-communities from a pool of pseudo-species, i.e. simulated (virtual) species 61 62 characterised by a unique thermal niche ranging from strict stenotherms (species that live in a 63 relatively restricted range of temperature) to universal eurytherms (species adapted to extreme 64 temperature variations) and from psychrophiles (organisms that live at cold temperatures) to 65 thermophiles (organisms that operate at warm temperatures)¹⁴. Only pseudo-species that were able 66 to withstand the local thermal regime and its temporal fluctuations occupied a given oceanic region and constituted a pseudo-community. We therefore focused on climate-induced long-term changes 67 68 (including ACSs) that originate from changes in the thermal regime and not shifts induced by other environmental parameters²⁰ (e.g. nutrients, salinity, oxygen) or triggered by anthropogenic pressures 69 70 (e.g. fishing, eutrophication and pollution)².

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72 We first tested whether our framework provided valid predictions, by comparing predicted long-term 73 changes in pseudo-communities with observed communities in 14 marine ecoregions spanning from 74 tropical to polar oceans (Pacific, Atlantic and Southern Oceans) and seas (Adriatic, Ligurian, North and 75 Baltic Seas) and based on zooplankton (11 ecosystems), decapods (1 ecosystem) and/or fish (4 76 ecosystems; Supplementary Tables 2-3 and Supplementary Figure 1). For each observed community 77 we performed a standardised Principal Components Analysis (PCA) on a matrix years x biological 78 variables (e.g. species abundance, biomass, or size fraction) and retained the first 2 Principal 79 Components to investigate their long-term changes (Obs-PC1-2s). In each system, 10000 PCAs were 80 also performed on 10000 pseudo-communities, each resulting from different pseudo-species associations simulated with METAL (Methods); we retained the 10000 Pred-PC1-2s¹⁴. We provide an 81 82 illustrative case-example here for the North Sea (Figure 1). Here, the first PC shows a pronounced 83 change at the end of the 1980s for 42% of taxa, and a simulated first PC also exhibits the same pattern 84 for 72% of the pseudo-species; both PCs were highly correlated (Figure 1a-b,e-f; r=0.83,p=0.01,n=50).

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The inspection of observed and predicted long-term changes in the community and their associated 86 87 mean correlations shows remarkably good prediction capability for every area, except for the highly dynamic and heterogeneous²¹ Western Pacific Transition Zone (Figure 2; Supplementary Table 4). 88 89 When the number of pseudo-species was high in a given system, variability in the METAL predictions 90 was reduced (Figure 2a-n). Note that long-term changes shown in the figure are the examples showing 91 the highest correlation between a given observed PC and predicted PCs. As might be expected, some 92 observed PCs were not highly correlated with predicted PCs (Supplementary Table 4), possibly because 93 some species may not react to temperature when their thermal optimum coincides with the mean local thermal regime^{14,22} or they may be more sensitive to other forcing (e.g. anthropogenic pressure, 94 other ecological factors, biotic interactions or local complex hydrodynamics)^{4,20,21,23}. That is why the 95 climatic signal identified by the PCAs was sometimes associated with PC1 or PC2. Random time series 96 97 with and without autocorrelation were generated for each system and analysed in the same way 98 (Methods). Simulated Pred-PC1-2s from these null models exhibited a pronounced variability in each 99 system, far above those originating from METAL (Supplementary Figure 2 *versus* Figure 2a-n). All mean 100 correlations were below those expected from METAL, with the exception of the HOT time series. This 101 result reveals the importance of using multi-decadal time series as shorter ones (e.g. HOT) may be 102 highly influenced by temporal autocorrelation²⁴, a mathematical effect enhanced when the number of 103 years is low.

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105 As in Figure 1a-b, the number of species influenced by temperature varies among systems, which 106 explains why the climatic signal can be detected either in PC1 or PC2 (Figure 2; Supplementary Table 107 4). Therefore, to consider the full complexity of the signal, we used the first 2 predicted PCs (mean 108 Pred-PC1-2, averaged over 10000 simulated PCs; Figure 2a-n) and applied a regression (Methods) that 109 explained 50.4% (r=0.71,p<0.01,n=567) of the total variance of all observed long-term changes in the 110 14 ecoregions (red Obs-PCs; Figure 2a-o). Since predicted pelagic communities are completely 111 independent from the measured communities, correlations are remarkably high. This suggests that 112 the METAL theory indeed captures the main drivers of changes. We also examined the correlations 113 between observations and predictions from 10000 simulations based on (i) METAL, random time series (ii) with and (iii) without autocorrelation. Although some correlations may be high with random time 114 115 series, especially when they are autocorrelated²⁴, correlations based on the METAL theory were 116 substantially higher (Figure 2p).

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118 Higher residual variability was observed occasionally in some areas such as in the Western Pacific 119 Transition Zone (Fig. 2g) and may reflect any of three main causes. First, it may be related to local 120 environmental complexity that is not fully resolved in our model. Future improvements of the METAL theory may help reduce this variability by including further ecological factors²⁰. At present however, 121 122 ecological dimensions of interest are rarely available on a year-to-year basis. Second, it is likely that 123 many marine ecosystems, especially coastal ones, are also influenced by human-induced factors such 124 as overfishing, eutrophication and pollution, and these probably affect the biological composition of 125 communities². Third, it is possible that uncertainties in sampling procedures significantly affect the 126 time series, although the PCA helped to reduce this variance¹⁴.

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Next, we tested the capability of our framework to reveal large-scale community changes, including ACSs, by combining all 14 ecoregions (Figure 3). To extract the overall bio-variability, we performed 'global' PCAs on the first two Pred-PCs extracted on (i) simulated (METAL and the null model based on autocorrelated time series) and (ii) observed communities for the 14 systems (14 systems x 2 PCs = 28 variables for each PCA); therefore for this analysis we used all first 2 observed and predicted PCs, which 133 represented the full set of interactions within the observed and predicted PCs (Supplementary Table 134 5). We chose the period 1960-2007 because it had less than 50% missing data per year in each time 135 series (Supplementary Figure 3). We performed this procedure in two ways: (i) one 'global' PCA based 136 on the average of all 10000 PC1-2s for each system to calculate the correlation between observations 137 and predictions from METAL, and (ii) 10000 'global' PCAs to assess the variability of long-term changes 138 (METAL and the null model based on autocorrelated time series). The first global PC originating from 139 observed communities was highly correlated (r=0.87) with the first global PC derived from the average 140 of the 10000 theoretical communities (Figure 3a). Predicted and observed PC2s and PC3s were also significantly correlated, although at a lower level (Figure 3b-c). METAL predictions were much less 141 142 variable than predictions based on the null model (Figure 3a-c, green versus blue curves).

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144 We then identified ACSs by calculating an Abrupt Shift Detection (ASD) algorithm on the 10000 global 145 PC1-3s (Methods). In our North Sea example, the algorithm detects a significant shift (i.e. value higher 146 than 3) circa 1987 for both predicted and observed first PCs (Figure 1c-d). For global PCs, the first two 147 observed and predicted PCs showed significant ACSs at the end of the 1980s and 1990s respectively 148 (Figure 3d-e). Interestingly, predicted (blue curves) ACSs occurred one year before observed ACSs (red 149 curves), a result possibly explained by the inertia related to species' life cycles¹⁷. This analysis shows 150 that the most frequent (but not necessarily the most intense) shift in the ecoregions coincided with the well-documented events of the late 1980s (Figure 3a,d)^{3,5,6}. Although they were not significant, we 151 152 detected acceleration phases on both third predicted and observed PCs (Figure 3c,f). Note that the well documented 1976/77 ACS¹⁶ was not significant globally, probably because it was only observed in 153 154 the East Pacific (Figure 2k). No significant trend was observed on global PCs based on autocorrelated 155 time series (Figure 3d-f, green curves). These results suggest that METAL can predict a substantial part 156 of long-term community change, including ACSs.

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We then applied our ASD algorithm to the whole ocean for the period 1960-2015, covering many areas 158 159 and years not biologically monitored. For this analysis, we did not perform any PCA but applied our 160 algorithm to pseudo-species and retained only ACSs when they involved half or more pseudo-species for a given location and year. Our analysis suggests that ACSs of relevant magnitude may occur every 161 162 year, but in a limited part of the ocean (~2.8%), involving on average over 10 million km² of ocean per 163 year (Figure 4a and Supplementary Figure 4). Some periods had geographically limited ACSs (e.g. 0.89 164 million km² for 1984-1987) whereas others carried more extensive ones (e.g. 50.5 million km² for 2012-165 2015). Widespread predicted ACSs were always observed after El Niño events (e.g. weak El Niño 166 episode of 1977-1978 and very strong episodes of 1997-1998 and 2015-2016) but not all El Niño events led to widespread ACS predictions (e.g. very strong episodes of 1982-1983; Figure 4a). Interestingly, 167

the late-1980s ACS, so frequently found in areas where monitoring took place^{3-7,25,26}, was not predicted 168 169 on a global scale. Despite similar strength in the two strong El Niño events 1997-1998 and 2015-2016, 170 the spatial extent of the predicted ACSs was very different, the recent one being more widespread (50 171 million km² circa 2014 versus 29 million km² circa 1999). The mean magnitude of ACSs increased 172 substantially after the mid-2000s with a peak circa 2012 (2010-2013)(Figure 4b). When both spatial 173 extent (here number of geographical cells) and magnitude were combined, an unprecedented shift (5 174 and 3 times the average extent and magnitude, respectively) took place after 2010 with a maximum 175 ~2014 (2012-2015)(Figure 4c). Our null model (Figure 3d-f) suggests that such an ACS at the end of the 176 time series is unlikely to be an artifact as is sometimes reported with other techniques³ (Methods).

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178 We investigated the relationships between predicted ACSs and observed changes in climate using 6 179 parameters measured at a global scale: annual Sea Level Pressure, meridional and zonal wind, wind 180 intensity, cloudiness, and Sea Surface Temperature (SST) (Methods). Using maps of ACSs and climatic 181 shifts calculated for each year (Supplementary Figures 4-5), we found significant correlations 182 (Supplementary Table 6) between long-term changes in the spatial extent of predicted ACSs and the observed shifts from 1960 to 2015 in atmospheric pressure (r=0.69,p_{ACF}<0.01,n=53), atmospheric 183 184 circulation variables (r=0.54-0.57,p_{ACF}<0.01,n=53) and, as expected, with annual SST 185 (r=0.97,p_{ACF}<0.01,n=53). No significant correlation was found with cloudiness. These results identify a 186 strong link between the spatial extent of predicted ACSs and climatic shifts in atmospheric circulation 187 and SST.

188

189 We then focused on 5 time periods: 1975-1979, 1985-1989 and 1995-1999 because these include already documented ACS^{3-7,16,25}, 2005-2009 because it is an example of a relatively stable period, and 190 191 the period 2010-2014 because of its exceptional nature (Figure 5). Note that these periods integrate a 192 larger number of years in the calculation of the abruptness index (e.g. 2010-2014 is based on 2008-193 2015 and similarly for other periods; Methods). The 2014-2015 expected ACS, precisely detected by 194 the visual inspection of Supplementary Figure 4, is much more intense and widespread than previous 195 ones (Figures 4-5), encompassing the recently observed meteo-oceanic anomalies, the Northeast 196 Pacific warm and the central North-Atlantic cold blobs, and including many areas of the Arctic 197 Ocean^{8,27,28} (Figure 5). Although changes in the North Atlantic and Pacific Oceans resulted in part from 198 changes in atmospheric circulation and its influence on the regional thermal regime, changes in the 199 Arctic result mainly from abrupt shifts in annual SST (Figure 5e, j, Supplementary Figure 6).

200

201 Our framework provides an explanation for long-term biological changes and ACSs. Each species 202 responds individually, its response depending upon the interaction between its thermal niche and

fluctuations in the thermal environment¹⁴. The close correspondence between shifts in theoretical and 203 observed communities supports the METAL theory¹⁴ and provides a useful system for predicting 204 205 climate/temperature-induced ACS at the community scale. However, there might be large unexpected 206 events such as the collapse or the explosive growth of some populations (a phenomenon known as 207 black-swan events²⁹) that may not be predicted with this theory. Our perception of the spatial extent 208 of an ACS has been severely limited by a paucity and unrepresentative coverage of observing systems. 209 Most marine communities are hidden from earth observation tools and developing an adequate 210 monitoring coverage for the entire ocean is logistically impossible. Our framework could therefore be 211 meshed with existing monitoring programmes to provide a macroscopic tool for ocean sampling to 212 identify regions that may develop ACSs and to alert us to potential biological perturbations that may affect ecosystem goods and services³⁰. In addition, our framework warns us that the large and 213 214 unprecedented ACS predicted to have occurred in 2014-2015 may have substantial ecological consequences^{27,30} throughout the Northern Hemisphere, including the Arctic, an area changing at an 215 216 unprecedented pace due to rapid melting of ice⁸. Finally, our study alerts us to the potential for an 217 increase in the size and consequences of future ACS events as the world warms in response to global 218 climate change. Even though it will remain difficult to predict ACSs, both because uncertainties and the simple fact that some events may remain unpredictable^{31,32}, the ability to forecast putative ACS 219 220 events is an important development in our understanding of climate change biology.

221

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231

232 Author contributions

233 G.B. conceived the study; G.B., A.C., A.A., E.G., J.C., S.C. and all co-authors compiled the data and G.B.

analysed the data. G.B. wrote the (initial draft) paper. G.B., A.C., A.A., P.C.R., E.G., J.C., R.R.K., S.O., S.C.,

- 235 M.E. and all other co-authors discussed the results and contributed to the paper writing.
- 236

237 Additional information

 accompanies this paper at www.nature.com. Reprints and permissions information are available online at www.nature.com/reprints. Our framework is freely accessible to interested scientists and manager (http://metaltheory.weebly.com/). Literature cited Boero, F. <i>et al.</i> From biodiversity and ecosystem functioning to the roots of ecological complexity. <i>L</i>:101-109 (2004) Scheffer, M. <i>Critical transitions in nature and society.</i> (Princeton University Press, 2009) Reid, P. C. <i>et al.</i> Global impacts of the 1980s regime shift. <i>Global Change Biology</i> 22, 682-703 doi:10.1111/gciol.2016 (2016) Greene, C. H., Pershing, A. J., Cronin, T. M. & Ceci, N. Arctic climate change and its impacts of the ecology of the North Atlantic. <i>Ecology</i> 89, 524-538 (2008) Conversi, A. <i>et al.</i> The Mediterranean Sea regime shift at the end of the 1980s. <i>PLOS one</i> 5, 1-15 (2010) Beaugrand, G. <i>et al.</i> Synchronous marine pelagic regime shifts in the Northern Hemisphere <i>Philosophical Tansactions of the Royal Society B: Biological Sciences</i> 370, 20130277 doi:10.1098/rstb.2013.0272 (2014) Arctic Council. Arctic Resilience Report., (Stockholm Environment Institute and Stockholm, 2016) Arctic Council. Arctic Resilience Report., (Stockholm Environment Institute and Stockholm, 2016) Di Lorenzo, E. <i>et al.</i> Central Pacific El Niño and decadal climate change in the North Pacific Trophic levels and weather. <i>Nature</i> 347, 753-755 (1990) Richardson, A. J. & Schoeman, D. S. Climate impact on plankton ecosystems inte northesa trophic aceace. <i>Biology Letters</i> 7, 702-755 (2010) Aebischer, N. J., Coulson, J. C. & Colebrook, J. M. Parallel long-term trends acrossfour marins trophic levels and weather. <i>Nature</i> 347, 753-755 (1990) Richardson, A. J. & Schoeman, D. S. Climate impact on plankton ecosystems inte northesa trophic levels and we	238	The au	The authors declare no competing financial interests. Supplementary information									
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319

320 Figure legends

321 Figure 1 | Long-term biological changes and abrupt community shifts (ACSs) for both the observed

322 community and a simulated pseudo-community in the North Sea. a-b. Long-term changes of the

323 first principal components (PCs) and in biological variables related to them (i.e. absolute values of the

- normalized eigenvector higher than 0.6; blue): (a) observed species and (b) simulated pseudo-
- 325 species. The first PC, considered to reflect major changes in community structure, is in black for
- 326 observed taxa (**a**,**e**) and red (**b**,**e**) for simulated pseudo-species. Taxa that were related to the
- 327 observed first PC were Calanus finmarchicus (negative relationship, -), C. helgolandicus (positive
- 328 relationship, +), Candacia armata (+), Centropages typicus (+), Corycaeus spp. (+), and Oithona spp. (-

- 329). Ten pseudo-species were related to the simulated first PC. The green band shows the timing of the
- ACS revealed in pannels **c-d**. **c-d**. Detection of ACSs for the first PC based on (**c**) the observed
- 331 community and (d) the simulated pseudo-community. The dashed red horizontal line indicates the
- threshold of 3 used throughout this study. **e-f**. Long-term observed (black) and simulated (red) first
- PCs (e) and their relationships (f). This ecosystem, and most biological systems considered in this
- 334 study (except HOT, Southern Ocean and San Francisco Bay) were also analysed in detail in
- Beaugrand¹⁴ and Beaugrand and colleagues⁶, respectively.

Figure 2 | **Predicted (grey) and observed (red) long-term community changes for 14 systems.**

- 337 Principal components were standardised between -1 and 1. Pred-PC: 10000 Principal Components
- 338 (grey) based on 10000 simulated communities. Obs-PC: Principal Component based on observed
- communities (red). **a**. North Sea (Pred-PC1s and Obs-PC1), **b**. Baltic Sea (Pred-PC1s and Obs-PC1), **c**.
- 340 Adriatic Sea (Pred-PC1s and Obs-PC1), d. Ligurian Sea (Pred-PC2s and Obs-PC1), e. Northwest
- Atlantic, southern area (Pred-PC1s and Obs-PC2), f. Northwest Atlantic, northern area (Pred-PC1s and
- 342 Obs-PC1), g. West Pacific Transition zone (Pred-PC1s and Obs-PC1), h. Oyashio (Pred-PC1s and Obs-
- PC1), i. CALCOFI (Pred-PC1s and Obs-PC1), j. San Francisco Bay (Pred-PC1s and Obs-PC1), k. East
- Pacific region (Pred-PC1s and Obs-PC1), I. West Pacific region (Pred-PC1s and Obs-PC2), m. HOT
- 345 (Pred-PC1s and Obs-PC2), n. Antarctic Peninsula area (Pred-PC1s and Obs-PC2). a-n. Linear
- 346 correlations (r_m) were calculated between the average of the 10000 predicted against the observed
- 347 community PC. o. Long-term community shifts predicted from a regression on principal components,
- 348 using the first 2 Pred-PCs from the 14 systems (averaged from the 10000 first 2 PCs). Observed long-
- term community shifts were Obs-PCs chosen in pannels **a-n**. **p**. Histograms of the 10000 correlations
- 350 between selected Obs-PCs and predictions based on the first 2 Pred-PCs from (i) the null model
- 351 based on random time series (green), (ii) randomly generated time series with an order-1
- autocorrelation ≥ 0.5 (blue), and (iii) the METAL theory (red). Biological variables that are considered
- in each site are indicated by the letters **D** (benthic decapods), **Z** (zooplankton), and **F** (Fish). Biological
- variables are indicated in the Methods. x|y:x is the number of pseudo-species used in METAL and y
- is the number of time periods (1 means annual value). Multiplicating x and y gives the total numberof variables.

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358 Figure 3 | Comparisons of long-term observed (red) and predicted (blue and green; 10000

- 359 simulations) community shifts, all ecoregions combined. Predictions from the METAL theory are in
- 360 blue and predictions from a null model with autocorrelation in green. (a) First PC: predicted and
- 361 observed long-term changes in communities. (b) Second PC: predicted and observed long-term
- 362 changes in communities. (c) Third PC: predicted and observed long-term changes in communities.

- 363 Index of abruptness in predicted and observed communities: (d) First PC. (e) Second PC. (f) Third PC.
- 364 Correlation (r), probability of significance without (p) and with (p_{ACF}) correction for temporal
- autocorrelation, and degree of freedom (n) are indicated in pannels **a**, **b** and **c** and correspond to the
- 366 correlation calculated between observations and METAL predictions when all local PCs are averaged.
- 367 In **d-f**, the wide blue (METAL) and green (null model) curves correspond to the median of the 10000
- 368 simulations and the lower and upper part, the 5th and 95th percentiles, respectively.
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370 Figure 4 | Predicted long-term variation of Abrupt Community Shifts (ACSs) in the global ocean. (a)

- 371 spatial extent, (b) magnitude and (c) spatial extent and magnitude of ACS. Curves in red are order-1
- 372 moving average of predicted values (blue bars) (Methods). Thin-dashed, thin-solid and thick red
- arrows display weak, moderate, and strong El Niño events, 'E' = super El-Niño events. Thin and thick
- blue arrows highlight moderate and strong La Niña events.
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376 Figure 5 | Predicted Abrupt Community Shifts (ACSs; a-e) and climatic shifts (f-j) during the period 377 1960-2015 with a focus on the years 1975-1979 (a and f), 1985-1989 (b and g), 1995-1999 (c and h), 378 2005-2009 (d and i) and 2010-2014 (e and j). Colour bars are percentage of individual time series that 379 show a significant shift (threshold>3). For ACSs, 50% means that half of the pseudo-species exhibited 380 a significant shift for a given pseudo-community. For climatic shifts, 50% means that half of the climate 381 parameters (3 out of 6 parameters) displayed a significant shift. White areas are regions with no shift. 382 When the percentage of shifts is >0, the percentage is indicated by a colour: blue and red for low and 383 high percentage, respectively. The six climatic parameters are: annual Sea Level Pressure (SLP), 384 meridional wind, zonal wind, wind intensity, cloudiness and SST. The spatial extent of ACSs increases 385 when the climatic shifts are more widespread. Individual maps of all predicted ACSs and observed climatic shifts are displayed in Supplementary Figures 4-5. Black arrow: direction and intensity of mean 386 387 annual wind (1960-2015). black line: isobar based on mean annual SLP (1960-2015).





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405 Figure 2 |







412 Figure 4 |





