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1   **A predictive timeline of wildlife population collapse**

2   Francesco Cerini [1,*], Dylan Z. Childs[2], Christopher F. Clements[1]

3   1 School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, UK

4   2 School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK.

5   **emails** - Francesco Cerini: francesco.cerini@bristol.ac.uk *corresponding author

6   Dylan Z. Childs: d.childs@sheffield.ac.uk

7   Christopher F. Clements: c.clements@bristol.ac.uk

12   **Abstract**

13   Contemporary rates of biodiversity decline emphasize the need for reliable ecological forecasting, but current

14   methods vary in their ability to predict the declines of real-world populations. Acknowledging that stressors

15   effects start at the individual level, and that it is the sum of these individual-level effects that drives populations

16   to collapse, shifts the focus of predictive ecology away from using predominantly abundance data. Doing so

17   opens new opportunities to develop predictive frameworks that utilize increasingly available multi-dimen-

18   sional data, which have previously been overlooked for ecological forecasting. Here, we propose that stressed

19   populations will exhibit a predictable sequence of observable changes through time: changes in individuals'

20   behaviour will occur as the first sign of increasing stress, followed by changes in fitness related morphological

21   traits, shifts in the dynamics (e.g. birth rates) of populations, and finally abundance declines. We discuss how

22   monitoring the sequential appearance of these signals may allow us to discern whether a population is increas-

23   ingly at risk of collapse, or is adapting in the face of environmental change, providing a conceptual framework

24   to develop new forecasting methods which combine multidimensional (e.g. behaviour, morphology, life his-

25   tory and abundance) data.

26

1. INTRODUCTION

Extinction rates over the last century have been estimated to be higher than at any point in recent history, with human activity identified as the predominant driver of this "sixth mass extinction"[1]. In addition to its positive effects on human wellbeing and culture[2], biodiversity underpins the stability and resilience of ecological systems on which humanity relies for food, fresh water, and clean air[3]. At the root of human-induced extinctions are a suite of stressors - stimuli creating a physiologically demanding or life-threatening situation for an organism - such as habitat loss, pollution, overharvesting, and climatic change[4,5]. Such stressors can drive declines and erode a population's ability to recover in the face of disturbances, increasing the probability of population collapse[6]. Indeed, multi-faceted pressures can be self-reinforcing, driving rapid collapses – the so-called extinction vortex[7,8]. Consequently, we are at a critical point for ecosystem management where, to preserve biodiversity and ecosystem services, we need to reliably detect not only what systems are being most impacted by anthropogenic stressors, but which are most at risk of collapse[9].

This need has driven the development of predictive methods that aim to infer the risk of population collapse, ranging from classical Population Viability Analyses (PVA[10]) to more recently developed Early Warning Signals (EWS[9–11]). However, the difficulty of surveying wild populations, together with economic limitations[12], often results in noisy and short time series which can detrimentally affect the accuracy of such predictive tools[13–15]. Most importantly, these methods have neglected other potentially powerful diagnostic features that theory and evidence suggest should be impacted by increasing environmental pressures and thus could act as additional indicators of approaching collapse. Modern frameworks converge on the idea that to improve our ability of forecasting extinctions we need to take into account the role that phenotypic plasticity (and its interaction with adaptative evolution[16]) plays in buffering the current environmental changes. In fact, the final decline of a population to extinction is a manifestation of a host of changes that occur first at the individual level, encompassing their phenotypic plasticity, and then – when a high enough proportion of the population exhibit similar changes – affect the dynamics of that population. Recognising and understanding such connections between organization scales (e.g. individual, population, community) has led to significant breakthroughs in ecology[17]. For example the metabolic theory of ecology has shown how individual metabolism scales to

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54 reproductive performance and population dynamics[18,19]. Such theoretical models have contributed to popula-

55 tion management and conservation[20–22], but their suitability for applied ecological research is occasionally

56 criticised[23–25] and they are limited to the informative power of a few parameters (e.g. selected temperature and

57 body mass data[26]). Moreover, current implementation of metabolic theory overlooks the power of actively

58 monitoring the populations in a way to update predictions as new data become available. A more informative

59 approach lies within the continuous measurements of multivariate indicators of change in conditions, to con-

60 sider how environmental pressure shapes different facets of individuals and populations through time.

61

62 An individual's physiology is the key mechanism through which it detects and respond to environmental

63 change; for example, stress hormone production is the initial trigger of phenotypic change[27]. Whilst using such

64 physiological measures as tools to identify at-risk populations certainly has merit[28], collecting data to achieve

65 this requires tracking physiological parameters across multiple individuals, often an intrusive and resource-

66 intensive task. Rather, focusing on the easily detectable downstream effects of these physiological changes

67 provides individual-based data on the effects of stressors. These downstream effects could include changes in

68 the behaviour of individuals[29], their morphologies, and/or life history traits[30], alongside traditional abundance-

69 based measures of extinction risk[31]. Gathering such multivariate information has historically been highly chal-

70 lenging in the natural world and multidimensional time series datasets for stressed populations are currently

71 very rare. Nevertheless, recent technological advancements in data-collection methods now provide the op-

72 portunity to generate high throughput information on these multiple features of populations with a relatively

73 low cost-benefit ratio[32,33]. However, what is still missing is a conceptual framework that explicitly shows how

74 such multidimensional data are related to each other, and how they can be used to discern whether a population

75 is increasingly at risk of collapse or is adapting in the face of environmental change.

76

77 The effect of increasing stressor intensity on a population propagates from the individual to the population

78 level via a successive series of responses (here referred to as "signals of stress"). We refer to "stress" as the

79 process whereby an organism reacts to stressors[5]. The individual-level responses necessarily take place (and

80 are observable) over smaller time scales than population-level signals; individuals' behaviour or morphology

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81 can change during their lifespan, while the effect of stressors on the population abundance trends will be ob-

82 servable (except in face of an unpredictable extreme mortality event such as a wildfire) after one or more

83 generations. This individual-to-population approach allows us to use individuals' stress responses as early

84 indicators of change in population conditions, and to measure the impacts of the stressors in multiple dimen-

85 sions simultaneously. Such an approach expands on recent work in the field of EWS, which consider abun-

86 dance based EWS and shifts in the mean body size of the population simultaneously, leading to an increase in

87 the overall predictive power[34,35]. However, these approaches ignore the fact that such signals are not necessarily

88 expected to change concurrently, but rather may occur sequentially as individuals' plasticity buffers them

89 against negative environmental conditions. Considering this temporal aspect in the occurrence of individual-

90 to-population level stress responses offers the opportunity to develop more effective forecasting tools which

91 make use of increasingly available data.

92

93 ## 2. THE TIMELINE TO COLLAPSE

94 We define the "timeline to collapse" as the temporal sequence of signals that can be observed by monitoring

95 multiple facets of a population which is driven toward extinction by a continuously increasing pressure (Figure

96 1). Individuals in a population, whilst experiencing similar unfavourable abiotic or biotic conditions (e.g. in-

97 creasing resource scarcity, pollution, etc; Figure 1a), can respond to these pressures in different ways, primarily

98 through shifts in behaviour and/or morphological and life history traits. Behaviours, by their nature, are plastic

99 and subject to rapid changes in the face of novel stimuli[36]. Regardless of whether highly plastic behaviours are

100 sufficient to maintain fitness in the presence of stressors[37] or prove maladaptive[38], they represent the earliest

101 easily observable individual-level responses to sub-optimal environmental conditions (Figure 1b, Box 1). If

102 behavioural shifts cannot maintain optimal conditions for growth and reproduction, an individual will start to

103 change morphologically as it loses condition (e.g. through decreases in body mass, Figure 1c) or as it expresses

104 morphological adaptation/defences. Thus, morphological traits (e.g. mass, antipredatory features, symmetry,

105 Box 2) provide a secondary response to environmental stressors via adaptative physiology-driven changes

106 (both intra and inter-generational). As with behavioural changes, an individual can undergo such morpholog-

107 ical shifts for a given time as reaction to the environmental pressure, but it cannot do so indefinitely.

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108 Continuously changing conditions can push individuals to a limit morphology status (e.g. a minimum body

109 mass) needed for maintaining a minimal rate of metabolism[39]; if stressors keep growing over such threshold,

110 basic processes necessary to survive can be impacted. Thus, such morphological shifts can be concurrent with

111 or followed by decreases in reproduction (i.e. life history traits adjustments, Figure 1d) and/or increases in

112 mortality rates.

113

114 Declines in reproductive rates represent some of the last stages of adaptive plasticity in life history of long-

115 lived species[40], where resources are reallocated from reproduction to maintain the survival of the individual

116 whilst allowing for the possible exploitation of improved future conditions[41]. Conversely, short-lived organism

117 might be adapted to prioritize reproduction at the cost of survival in presence of stressors[42]; in such cases, a

118 growing environmental pressure would still put the next generation of offspring in unfavourable conditions

119 resulting in lower survival. Such life history traits modifications, whilst not as readily measurable as morpho-

120 logical or behaviour change, will have significant and detectable effects on population abundances observable

121 over longer (>1 generation) time frames. These may not necessarily lead to immediate population declines,

122 but can manifest as a loss of resilience potentially triggering EWS. Indeed, decreases in reproductive success

123 and increases in mortality may induce population abundance declines and subsequent rebounds (e.g. due to

124 density dependant reproduction, Figure 1d, e). If these changes drive the system toward a tipping point[43], this

125 phase of the timeline may result in a significant temporal trend in one or more statistical moments of population

126 abundance [31]. Indicators such as variance, autocorrelation, density ratio, and skewness of the abundance time

127 series can act as warning signals of collapse[9]. Such EWS have been criticised because of their high false pos-

128 itive rates[44], but observing them in the context of the timeline to collapse – i.e. after having already detected

129 changes in behaviours and traits – provides additional evidence to suggest such signals are true positives. In

130 fact, the slowly occurring life history changes inducing EWS represents the ultimate signals a population may

131 show before a continuous decline in abundance. If environmental stressors still increase after these signals –

132 and if individuals cannot move or migrate – diminishing demographic performance will drive sustained large

133 declines from the population abundance equilibrium state. (i.e. collapse, Figure 1e). At this point, a population

134 may be "committed to extinction", where genetic factors (e.g. inbreeding[45]) and demographic constraints (e.g.

135 Allee effect[46]) may mutually reinforce one another to rapidly propel it to extinction[7].

136

137 This temporal pattern of signals will necessarily develop at time scales relevant to the study organism and to

138 the rate of stressors increase, i.e. lifespans and generations rather than absolute time periods. For small inver-

139 tebrates, behavioural shifts may be observable over hours (e.g., *Daphnia* depth shifts[47]), while changes in

140 abundance may happen over days. For larger vertebrates, shifts in morphology may take place over months

141 (e.g., Steller sea lions weight loss[48]) whilst EWS and subsequent abundance declines may occur over years.

142 Regardless of the direction of the shifts and the stressor's nature, we expect the temporal sequence in the

143 typology of signals (behavioural, morphological, abundance; Figure 1) to remain broadly consistent.

144

145 **2.1. Framework details**

146 The timeline to collapse concept assumes continuously increasing stressor intensity – be that biotic or abiotic

147 – taking place over one or multiple generations (Figure 1a) such that a population is able to respond, rather

148 than sudden step-shifts in a stressor which may eradicate a population in the absence of any indicators[9]. More-

149 over, the framework assumes a stable initial phase of population dynamics (i.e. equilibrium population dynam-

150 ics[49]) against which signals of stress can be compared. When characterising the timeline, we identify the time

151 points when the population's average values of a given behaviour, trait and reproductive rate change signifi-

152 cantly from the values observed under stable conditions (T_{Bs}, T_{Ms} and T_{Ls} points, Figure 1), and the time points

153 when the plastic limits of change in the behaviour and morphology are reached (T_{Be} and T_{Me}, Figure 1), or

154 when the reproductive rate drops to zero (T_{Le}). Although such points may visually resemble "tipping points",

155 applying EWS theory to anticipate them is inappropriate, as there is currently no theory which suggests that

156 behavioural or trait metrics (which are not expected to pass through a tipping point) should show the critical

157 slowing down phenomenon required for EWS to be present[50].

158

159 Nevertheless, a stress-induced increase in the variance of these metrics among individuals and through time

160 may be expected, together with changes in the mean. When stressor intensity starts to increase, individuals'

161 responses will vary based on, for example, personality and past experience for behaviours[51], or genetic pre-

162 disposition for more or less plasticity in morphological and life history traits (e.g. due to intrinsic inter-indi-

163 vidual variability[52]). Such differential personality-and-physiology-based stress responses would initially lead

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164 to an increase in the variability around mean changes in behaviours, morphologies and reproductive output

165 (Figure 1). However, selection will soon homogenize these around the new (optimum) behaviour/trait values

166 that allow individuals to survive, or around the physiological limits (i.e. low variance around the new mean of

167 individuals, Figure 1). Although such patterns in the variance provide additional metrics to monitor[53], they are

168 less likely to contain information about the risk of population collapse; rather, we propose such information

169 lays in the temporal sequence of the different signals.

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171 Whilst the initiation time points of behavioural, morphological, life history and abundance shifts (T_{Bs}, T_{Ms}, T_{Ls}

172 and T_{As}, Figure 1) are expected to be sequential, the time intervals over which such shifts occur (I_B, I_M, I_L, and

173 I_A, Figure 1) may overlap. Indeed, changing a behaviour above a given threshold may require the use of energy

174 reserves which triggers changes in morphological traits. For example, for a seabird population (Figure 1),

175 increasing foraging distance may be the first response to decreasing food availability. Acquisition of additional

176 resources derived from greater foraging effort may be sufficient to compensate for this additional effort outside

177 the breeding season. However, if the food is needed to feed chicks[54], the individual may either i) fail to fully

178 replenish their energy stores (i.e. start to lose weight) or ii) decrease feeding rate to offspring to maintain their

179 ability to forage[54]. This will result in observing flight distance increasing together with declines in the body

180 weight of adults, offspring, or both (overlap among I_B and I_M, Figure 1). However, in other scenarios, we may

181 observe a clear temporal distinction between signals time intervals (i.e. no overlap among I_B and I_M). For

182 instance, in the presence of an invasive predator, a prey can go through an initial fast and discrete behavioural

183 change (e.g., a shift in microhabitat use[55]), followed by a morphological shift (e.g., change in body size due to

184 different conditions in the new microhabitat[56]), without any overlap between these two signals.

185

186 **2.2. Framework boundaries and scope**

187

188 The timeline to collapse concept builds upon work in different research areas, including behavioural ecology,

189 physiology and predictive ecology, and the recent suite of work on EWS[30,34]. However, whilst EWS are a

190 feature of the framework, we do not propose to apply critical slowing down theory to all signals of stress in

191 the timeline, nor to try predicting when shifts in behaviour, traits, or measures of population variability will

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192 occur. Rather, our focus is on describing the succession in time of different responses and how together these

193 might be used to infer approaching population collapse. The framework aims to holistically consider multiple,

194 often overlooked, types of data as tools for predictive ecology, and discriminate populations tending toward

195 extinction from those simply adapting in the face of change.

196

197 For instance, if whilst monitoring a bird population (e.g. with GPS tags) we observe the average flight distance

198 increasing and then plateauing at a given value (Figure 1B), we could misinterpret that value as the new be-

199 havioural optimum[16] reached by the individuals that are responding to the stressor level, whilst it could simply

200 represent the physiological plastic limit of that behaviour. Focus on a single measurement would lead to the

201 successive signals of stress – e.g. reduction in the body condition of the individuals triggered by the increasing

202 environmental pressure not sufficiently countered by the first response (Figure 1) – to be overlooked. In this

203 case, the multidimensional perspective reduces the risk of wrongly considering the population as adapting to

204 the new environmental conditions. Thus, successive signals act as increasing evidence that the behavioural,

205 morphological, or demographic changes are failing to ameliorate negative effects of increasing stressors as

206 each change is in turn more costly for an individual to implement.

207

208 Additionally, the time scale over which we observe the signals sequence can be a discriminant tool for dis-

209 cerning a collapsing population from one undergoing plastic or evolutionary adaptation[16,57]. Stressors changing

210 rapidly (i.e. within a generation) might create unsustainable conditions for individuals survival over one or a

211 few generations. When a population is under such critical rate of change[16], there will not be enough time for

212 adaptive evolution and thus evolutionary rescue[58] to happen. In such situations the individuals of the first

213 generation that encounter the stressor rely solely on the *a priori* (not shaped by selection) behavioural and

214 phenotypic plasticity to counter the growing environmental pressure (see Figure 1). The first two signals of

215 the timeline would thus be visible during the lifetime of the monitored individuals (e.g. intra-generation),

216 alerting practitioners that the plasticity of the current phenotypes is not enough to cope with the stressors

217 increase rate, and collapse is likely to happen. This "fast ramping stressor" scenario is the best suited for the

218 timeline application, and arguably represent the most pressing situation that many endangered species popula-

219 tions are currently facing[59,60].

220

221 Conversely, if environmental pressure changes slowly over multiple generations, traits may change continu-

222 ously in response due to adaptive evolution and phenotypic plasticity[16,61], and considering such slow changes

223 as early signals of collapse is misleading. The slowly increasing pressure can select phenotypic optima without

224 the population having to go necessarily through decline phases, and thus an intra-generational timeline should

225 not be observed. Nevertheless, with time a slow ramping stressor can push the optimum phenotype into a non-

226 viable space over which a catastrophic shift of the population to extinction and the related early warning signals

227 can be expected[62]. Thus, it is conceivable that the individuals of the generation encountering such a trait bound-

228 ary, induced by the stressor levels, may still display an intra-generational timeline to collapse. More theoretical

229 work is needed to resolve the predictions of this framework in such long time scales scenarios, by potentially

230 incorporating phenotypic plasticity and hereditability over multiple traits and evolutionary rescue theory[16,62].

231

232 **3. ECOLOGICAL INSIGHTS**

233 Whilst the temporal order of signals provides information on a population's future, *post hoc* analysis of be-

234 havioural and morphological shifts offers a means to characterise the stress responses of populations. We sug-

235 gest that the change in the mean values of behaviours or morphological traits between pre-stress (stable) con-

236 ditions and the onset of the next signal of stress (e.g. from when behaviours start to change to when body traits

237 begin to change) represents an "intrinsic stressor buffering capacity": a measure of the ability of a behaviour

238 or trait's plasticity to ameliorate stressors' pressure. Defining B_s and M_s as the mean values of a monitored

239 behavioural metric and morphological trait during stable conditions, and B_x and M_x their respective values at

240 the onset of the next buffering signal/level (Figure 1, Point 1 and 2), we can extract quantifiable ranges of

241 variation (ΔB for behaviour and ΔM for morphological trait, Figure 1).

242

243 From this framework, ΔB and ΔM could be calculated for traits that can undergo continuous shifts and com-

244 pared among different species and populations. For instance, nematodes and rotifers show extreme plasticity

245 in morphology (reductions of up to one-third of original body size[63]) to cope with long periods of environmen-

246 tal pressure (e.g. exsiccation of habitat). The resulting high value of ΔM would reflect the large amount of

247 pressure they can buffer by changing morphology before the eventual occurrence of demographic signals in

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248   the population. In contrast, e.g. amphibian species with limited drought resistance would display much lower

249   ΔM in comparison. Such plasticity proxies may be compared among different species to indicate which bio-

250   logical/ecological traits (group living vs solitary animals, bigger vs smaller dimensions, specialist vs generalist

251   etc.) are associated with stress resistance. Additionally, average ΔB and ΔM may vary among populations of

252   the same species, due to differences in biogeographic history and genetic structure (e.g. allelic heterozy-

253   gosity[64]), which may provide information on how such factors shape capacity to cope with stress. Such changes

254   will likely occur in multiple behaviours or traits simultaneously in order to cope with increasingly stressful

255   conditions, and thus measuring behaviours or traits in multiple dimensions (e.g. social interactions, distance

256   foraging occurs over, time spent inside burrow, etc.) would allow plasticity in multi-dimensions to be quanti-

257   fied, and tools such as those employed in the analysis of functional diversity could be readily applied to these

258   data[65].

259

260   **4. KEY QUESTIONS**

261   The timeline to collapse provides a conceptual framework to synthesize multiple types of data to help infer the

262   future dynamics of ecological systems. However, applying this to real-world populations requires identifying

263   appropriate data to monitor (behaviours, traits, abundances), measuring baselines against which change can be

264   quantified, and developing statistical tools to holistically consider these data simultaneously to provide robust

265   detections of increasing stress and possible forecasting techniques. Below we consider some of the key ques-

266   tions that must be answered to turn the conceptual timeline framework into an appliable pipeline for monitoring

267   and conservation management.

268

269   **4.1. How to select and acquire the data that are more indicative of stress?**

270   Some behaviours and morphological signals may provide general indicators of increasing stressor intensity

271   (e.g. increased dispersal for vagile species), but selecting signals that are relevant to the taxa of interest remains

272   key[66]. Expert knowledge can aid in this[67], identifying behaviours and traits that are most likely to change given

273   the nature of the stressor or, when the identity of the stressors is unknown, can provide general indicators of

274   an individual's condition. Ideally, behaviours and morphology measures that are easily collectable through

275   automated and non-invasive means are to be preferable. Many cutting-edge data collection tools can get

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frequent measures of such multivariate data needed to build accurate time series. For example, GPS tracking, biologging, acoustic monitoring, and photographic analysis are now able to extract data on behaviours and morphological traits, providing invaluable information even from a subset of the population[8,68–70] (Supplementary Material Table S1).

4.2. How can we define baselines?

A quantitative and/or qualitative definition of "normal" values for the identified behavioural, morphological, and abundance indicators is needed to pinpoint the moment in time when stress responses start (T_{Bs}, T_{Ms}, T_{Ls}, T_{As}, Figure 1). Defining such values in wild populations ideally requires long term monitoring data[71] on the multiple facets of a population under non-stressed conditions. In cases where the monitored populations have been already exposed to stressors for a period a time (i.e. no data in non-stressed conditions), one would need to select an arbitrary time gap from where to compare change, ideally a period when stressors levels were not changing. Such data will become progressively more available as remote sensing and technological advancements continue to automate data collection at large scale[72–74]. With these data on non-stressed/stable-stress condition populations, one can characterize the range of variation in the selected behaviours and morphological traits that, together with the abundance fluctuations, can be analysed to obtain means and upper and lower confidence intervals. In absence of such long term monitoring data, a comparative approach between populations experiencing different levels of stressors intensity could provide baseline values such as along a stress gradient[75] – a space-for-time substitution[54,76].

4.3. How can we handle the multivariate data to better forecast a population's future?

Regardless of how a baseline is defined, the big challenge ahead in the timeline application is understanding how to compare multivariate baseline data to observed changes in behaviours, traits, and abundances and how to use these signals to improve population collapse forecasting. Using normalisation and summation of multiple signals to improve predictive power has previously been done (e.g. combining morphology data with abundance EWS[34,77]), but this approach is not applicable to sequential signals. Keeping in mind the timeline sequence of signals, a possible partial approach may come from Metabolic Scaling Theory and derived mechanistic trait-driver models. One could monitor the trait distribution characteristics of a population under

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pressure, whereby a sudden variation in such quantities (e.g. individuals starting to lose biomass, the morphological signal) could be used to predict individual performance and how this will scale up to influence demography of populations (i.e. pre-emptively forecast the decrease in reproductive and survival potential[78]).

Other new approaches may lie within multivariate time series models[79] that account for the inter-dependencies between behaviour, traits, and abundance (e.g. how behaviour can influence morphology and vice versa). For instance, Multivariate Autoregressive State Space models[80] can use information on historical trajectories of multiple variables to forecast future values while accounting for multiple sources of uncertainty[81]. Alternatively, deep learning networks such as recurrent neural and temporal convolutional neural networks[82–84] could provide an obvious but more powerful approach to forecast future trends or changes in such variables[85], though these tools will require large amounts of data to train the models, which are only feasibly collected through automated means[73]. Once a suitable algorithm has been selected and trained on baseline data, the resulting model can be used to detect rare or anomalous dynamics in the multivariate space. Moreover, one could aim to generalize the prediction of collapse for new cases by training the models with the multidimensional data on past collapses of multiple populations from different species.

5. CAVEATS

The timeline to collapse concept necessarily makes assumptions about how stressors will impact populations. The first assumption is that stressors will increase over time (Figure 1), allowing populations to respond gradually to increases in environmental pressure. However, as with EWS and PVA, sudden and/or catastrophic "pulse" disturbances (drought, storms, fires etc.) may lead to significant changes in the abundance or distribution of a population without any warning. Moreover, even in cases of the assumed ramped disturbance, the mutable nature of biological systems may create situations where the sequence of signals may be different (e.g. body traits shift occurs first, triggering then behavioural shift[35]). Secondarily, we assume equilibrium dynamics for the abundance time series before collapse (i.e. assumption behind the EWSs), in addition to a stable optimum of behavioural and traits measurement (Figure 1). Although many vertebrate populations shows stability through time[49], chaotic trends are not uncommon among other groups (e.g. insects[86]). For such species, whose population dynamics can naturally undergo irregular boom and bust cycles, the definition of collapse is often problematic, and the application of the timeline concept in its current form might not be feasible. Furthermore,

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332 fully applying the framework requires studying species that show plastic and quantifiable behaviours and mor-

333 phological traits, where gathering data is easy at the individuals' level, and thus it may not be readily applicable

334 to sessile organisms, obligate parasite species, or plants and fungi without defining more clearly what consti-

335 tutes a behaviour likely to change in such systems. Focusing on group level responses (e.g. bleaching of An-

336 thozoa colonies) might help in those cases where assessing change would be hard in single individuals (e.g.

337 continuously monitoring behaviours of single polyps). Additionally, in limit cases where behavioural re-

338 sponses are hard to define, we believe that a partial application of the timeline concept (e.g., monitoring mor-

339 phological, life history traits and abundance data) will improve the predictive horizon of eventual collapses

340 compared to considering only abundance. Finally, although in this piece we decided to focus on more imme-

341 diately measurable traits shifts, we acknowledge that for taxa in seasonal environments, changes in phenology

342 can be considered as other potential signals to include in the timeline framework. Phenological shifts are well

343 known to be induced by e.g. climate change[87,88] but are often observed over long time periods (e.g. birds'

344 earlier arrival to breeding sites occurred over 20 years[89]).

345

346   6.   **CONCLUSION and Future directions**

347 Considering how anthropogenic stressors impact populations via changes in individual-level features provides

348 a key step forward in predicting population extinction. Doing so has allowed us to develop a conceptual frame-

349 work where the temporal aspect of stress signals can act as a corroborative tool to infer risk of population

350 collapse. The next steps to assessing the potential of this framework is to obtain complete and accurate datasets

351 covering the full suite of timeline components (see Box 3) for populations driven to collapse by increasing

352 stress. A *post hoc* analysis of the multivariate dynamics of such collapses would guide in understanding the

353 best approaches to use to forecast future ones. Experimental data from study models (e.g. micro-mesocosms

354 populations[90–92]) would be of invaluable help in this, whereby one could implement different disturbance sce-

355 narios[93] while accurately collecting the multidimensional data[73]. Future research should aim at relaxing some

356 of the current framework assumptions: e.g. investigating whether behavioural and trait changes might still

357 precede a collapse even if the system does not show equilibrium, but shifts toward alternative state of extinc-

358 tion. Nevertheless, the literature groundings of the timeline idea already provide a conceptual model for the

359 development of monitoring programs covering a broader spectrum of data than is typically considered by

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360   resource managers. Such a holistic view of how the behaviours, morphological features, and dynamics of pop-

361   ulations change as they become increasingly stressed offers hope of a step-shift in the accuracy of methods to

362   predict population declines, helping in the urgent fight against biodiversity loss.

363

364   **Acknowledgements**

367   **Author contribution statements**: CC and DC formulated the framework. FC developed the ideas, reviewed

368   the literature and wrote the first draft of the manuscript. All authors contributed substantially to revisions

369   **Competing interests**

370   The authors declare no competing interests.

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Figure captions:

679 **Figure 1**. Theoretical example of a timeline to collapse. We posit a population of seabirds inhabiting an area

680 where prey resources begin a continuous decline (a). The curves in panels b, c and d represent respectively the

681 average values of a behavioural and morphological trait, and the reproductive rate, calculated from a pool of

682 individuals in the population through time; the coloured shaded areas show the variance around the mean. The

683 red curve in panel e shows the abundance of the population. First a shift is observed in the behaviour (time

684 point T_{Bs}), where the average foraging distance increases (together with the variance) compared to the average

685 measured during stable conditions B_s (b). The foraging distance increase until it reaches a physiological limit

686 (time point T_{Be}), defining the time interval I_B where a continuous change is observable. After, or during I_B, we

687 observe a decrease in average body size (with increase in the variance) compared to that measured during

688 stable conditions M_s (c), at time T_{Ms}. The body size will change until its physiological limit (T_{Me}), defining the

689 time interval I_M. After or during I_M, the mean reproductive rate starts to show a declining trend and increase in

690 variance (time point T_{Ls}, d). The large fluctuations in the reproductive rate line want to represent possible

691 density dependence of the rate. The reproductive rate of the population will drop to zero at time point T_{Le},

692 defining the time interval I_L (d). During I_L, the abundance trend of population will show fluctuations, possibly

693 driving alterations in the pre-decline indicators such as Early Warning Signals that will start to be observable

694 from time point T_{As}, and will last until T_{Ae}, defining the time interval I_A. The dashed line separating panel d

695 and e exemplifies the direct effect that the first measure has on the latter. Subsequently, the continuous de-

696 creases in abundance (e) will begin at time point T_{Es}, and will end with the extinction of the population at time

697 T_{Ee}, lasting the time interval I_E. The first occurrence of the signals projected on the lower Time axis shows the

698 sequence in the category of observable signals of stress starting at the individuals' level (b, c, d) and propagat-

699 ing to the population level (e), defining the timeline to collapse. The small black dotted lines project the starting

700 point of the shifts in morphological traits and reproductive dynamics on the behavioural (point 1) and morpho-

701 logical trait (point 2) curves. Projected on the vertical axis, those points identify B_x and M_x: the values of

702 behavioural and morphological metrics at the time of the onset of the next signal along the timeline. The

703 interval of change (brackets) from the average values defines the intrinsic stress buffering capacities of that

704 behaviour (ΔB) and morphological trait (ΔM).
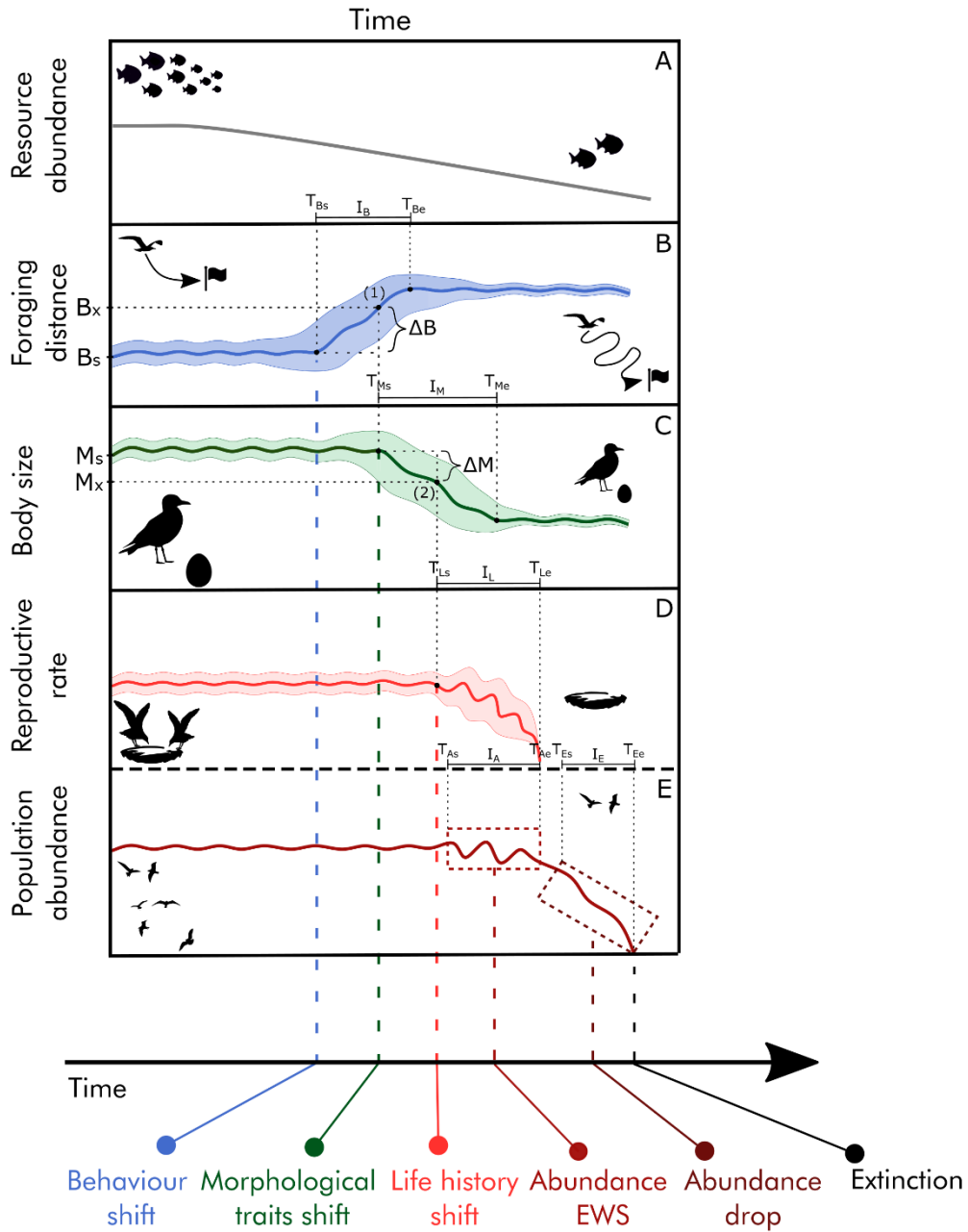
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707   **Boxes.**

708   **BOX 1. Overview of behavioural signals**

709   Behavioural changes are amongst the most rapid changes that individuals can perform to cope with sub-optimal

710   conditions[94]. Broadly, behaviours comprise movement and habitat use, foraging activities, reproductive and

711 social behaviours[29]. All these categories of behaviour can be modified by stressors; many studies on vagile

712 species show variation in e.g. foraging activity and dispersal of individuals in response to declining resource

713 availability[54,95], climatic change[96–98], and invasive species[99]. For instance, on Svalbard (Norway), a population

714 of ringed seals suffered a major reduction in sea-ice level resulting in fewer areas where the seals could feed

715 intensively. Subsequent monitoring of movement patterns showed that seals swam greater distances and dived

716 for longer periods (Box 1 Figure a, bars indicate standard error; data adapted from[96]). Among the different

717 responses, spatial movement constitutes perhaps the most easily observed and measurable signal of increasing

718 stress for vagile species, as data can often be captured remotely e.g. via GPS tracking or remote camera mon-

719 itoring, techniques which bridge taxa (vertebrate and invertebrates[100,101]) and realms (marine and terrestrial[70]).

720

721 In addition to movement patterns, individuals may react to stressors by altering rates of feeding activity and

722 typology (e.g. autotrophic vs heterotrophic), and rates of intra - and - interspecific interactions, including ef-

723 fects observed in social and communicative behaviours[102]. For example, temperature change is known to al-

724 ter filtering activities and valve opening periods in bivalves[103], as well as acting on in corals polyps expan-

725 sion[104]. Additionally, photosynthetic activity of corals can be affected by pollution[105]. Resource scarcity may

726 lead individuals to allocate energy to essential activities (e.g. foraging), decreasing actions not linked to sur-

727 vival, such as the engagement in territorial defence. Such a response was seen in multiple species of central

728 Indo-Pacific corallivorous butterfly fishes (*Chetodon* spp.) in the aftermath of a bleaching event in 2016

729 which led to a reduction in corals[76]. Observations suggested that the probability of both heterospecific and

730 conspecific aggressive encounters decreased significantly (Box 1 Figure b, Bars are 95% confidence inter-

731 vals; data adapted from[76]) as nutritional deficits increased the relative energetic cost of resource defence be-

732 haviour. Similarly, acoustically active insects and amphibians may change the acoustic properties of the mat-

733 ing signals in response to temperature change[106]. Moreover, anthropogenic noise can induce reductions in

734 whistles and echolocation click rates of social cetaceans[107].

735 The direction of change in behavioural metrics will vary depending on a species' environmental tolerance,

736 trophic level, and stressor type. Whilst a lack of resources may trigger increases in movement, the arrival of

737 an invasive predator may induce a prey species to reduce movement (to reduce encounter rates) or to shift

738 microhabitat use toward a more shelter-oriented strategy[108]. Environmental stressors may also increase the

739   variance in behavioural metrics, e.g. poor environmental conditions enhanced the variability of foraging trip

740   duration in young albatrosses[53].

741   When trying to identify and quantify significant behavioural change as response to stressors, a population's

742   ecological and biogeographical history must be considered. In fact, previous experience may play a critical

743   role in determining an individual's response to stressors. For instance, compared to naïve individuals, fishes

744   with previous experience of predation events showed stronger antipredator behaviours (e.g. decreasing swim-

745   ming activity) when they were represented with the chemical cues of the predator[109]. Likewise, the evolution-

746   ary history of a population can shape an individual's capacity to react to environmental pressure; lizard species

747   performed antipredatory behaviours in response to a new predatory snake if the lizards evolved with other

748   snake species which share similar predatory features (shape, chemical cues etc.) with the introduced preda-

749   tor[110].

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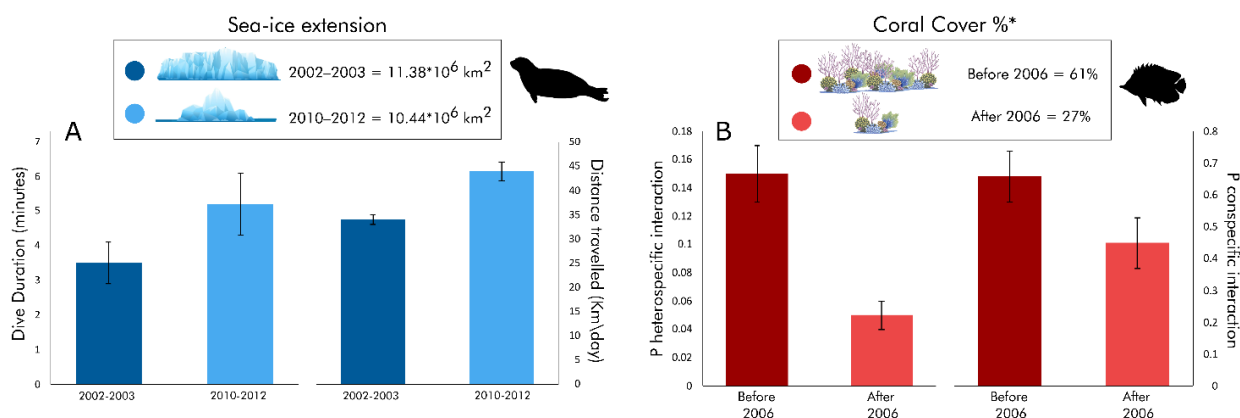
**BOX 2. Overview of morphological signals**

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754   To mitigate the effects of increasing stressors intensity individuals can respond to maximize survival and re-

755 productive output through changes in morphological and fitness-related life history traits[111]. Such changes are

756 driven by hormone responses, metabolic adjustments and resource re-allocation, and can include reductions in

757 body mass, decreases in growth, shifts in reproductive schedules, and antipredatory morphological trait ex-

758 pression. Here we focus on morphological shifts as they are more easily observable and measurable compared

759 to fitness related life history traits. For example, morphological features can be measured remotely through

760 photographic analysis, while measuring reproductive outputs or patterns of sexual maturity requires strict mon-

761 itoring with particular time periods (e.g. breeding seasons).

762   Environmental stressors substantially affect morphological trait distributions, both prior to or concurrent with

763 shifts in the demography and dynamics of a population[30,112]. The reduction in body size due to sub-optimal

764 food consumption is a general response to resources scarcity[48]. In numerous taxa, body size reduction is also

765 directly and indirectly induced by climatic change and habitat fragmentation[113–116]. For instance, a population

766 of polar bears from the Western Hudson Bay (Canada) was monitored between 1979-2004, a period where

767 sea-ice cover showed a trend toward earlier sea-ice breakup induced by climate change[117]. The study found

768 significant declines in mean adult female polar bear mass during this period (Box 2 Figure A, bars indicate

769 standard deviation, dashed line indicates fit of linear regression [r=-0.549, p<0.01]; data adapted from[117])

770 which strongly correlated with the progressively earlier dates of sea ice breakup.

771   Body size is a key trait that directly affects thermoregulation and rates of energy intake and utilization[114], and

772 has recently been suggested as a possible measure of population stability[92]. In fact, changes in body size of

773 diatoms algae preceded a regime shift in a lake ecosystem[118], and experimental populations exhibit the same

774 pattern, showing that – when resources decrease – declines in average body size precede declines in population

775 size[30]. In situations where longitudinal measures of body size/mass are available, change in individuals' growth

776 rates could be used as a potentially more accurate stress signal, since growth rate will respond more rapidly

777 compared to measures of mean body size. Indeed,[119]reported a decrease in the growth rate of individuals of

778 three sea turtle species in response to climatic stressors and anthropogenic degradation of their foraging areas.

779   Reductions in size is the most likely outcome of stress, although some stressors may lead to other patterns of

780   change. For instance, environmental pressures can lead to a decrease in defensive morphological traits: UV

781   light exposure in pregnant individuals of a freshwater cladoceran induced the reduction of antipredator spines

782   in their offspring, and subsequently increased predation risk for new-borns[120]. Conversely, the novel pressure

783   that an invasive predator puts on a native population can trigger increases in predator induced-defences[121].

784   Chemical pollutants can affect body symmetry, with pesticides used in hazelnut orchards leading to increased

785   fluctuating asymmetry in morphological traits linked to intraspecific interactions in lacertids (i.e. femoral

786   pores, Box 2 Figure B, bars indicate standard error, data adapted from[122]). Moreover, increasing fluctuating

787   asymmetry has been suggested as an indicator of loss of genetic variation prior to extinction[123].

788   This suite of responses, including (but not limited to) declining body mass/size, expression of chemical induced

789   antipredatory features, and asymmetry in meristic features will generally occur over (relative to the organism's

790   lifespan) longer time periods than rapid behavioural changes, but may still occur within the life span of an

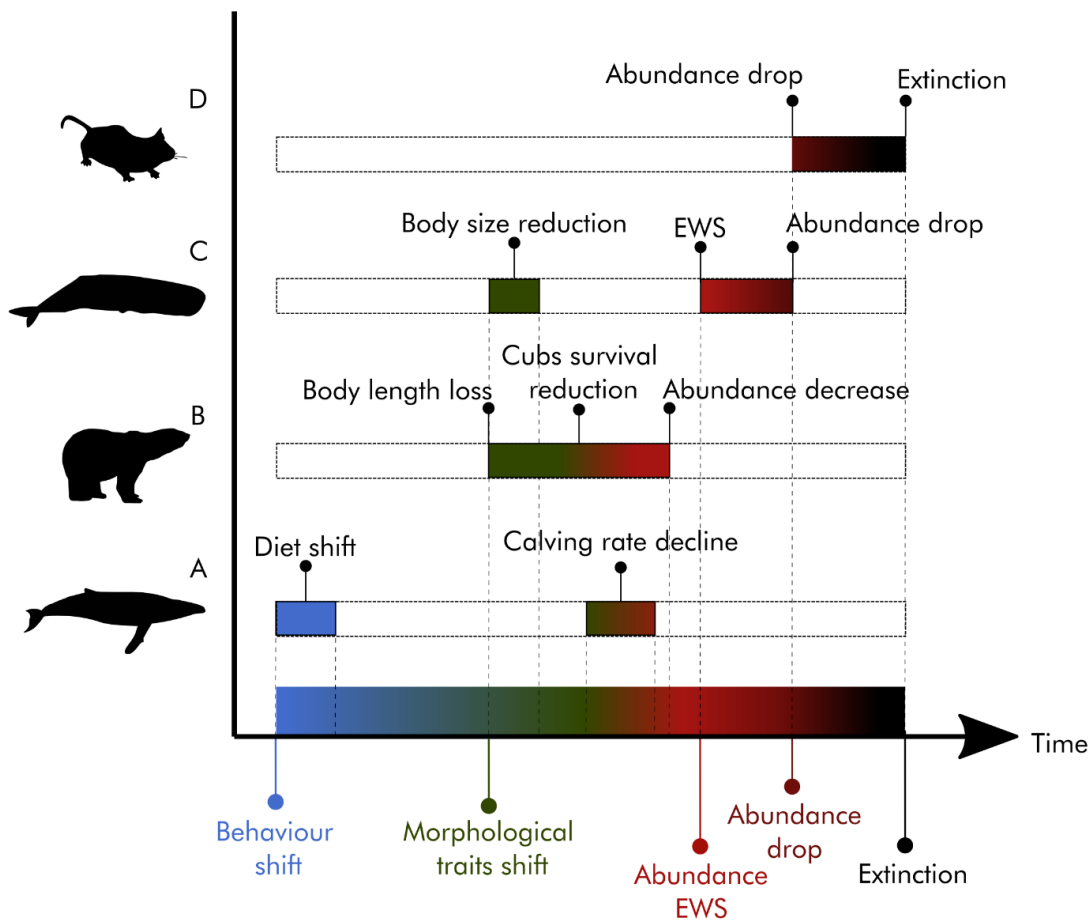791   individual (i.e. ≤1 generation), or across multiple sequential generations (e.g.[34]).

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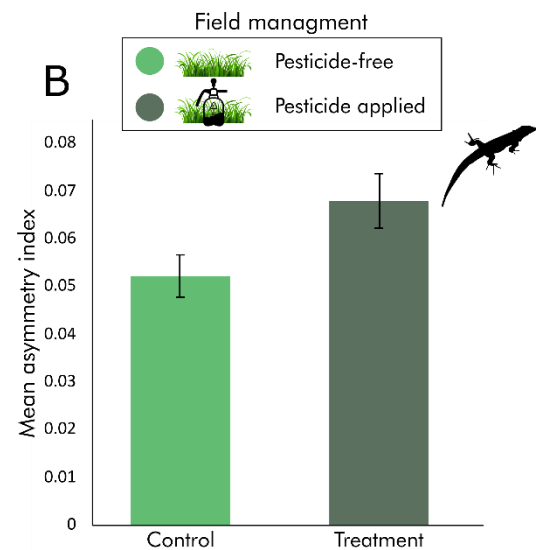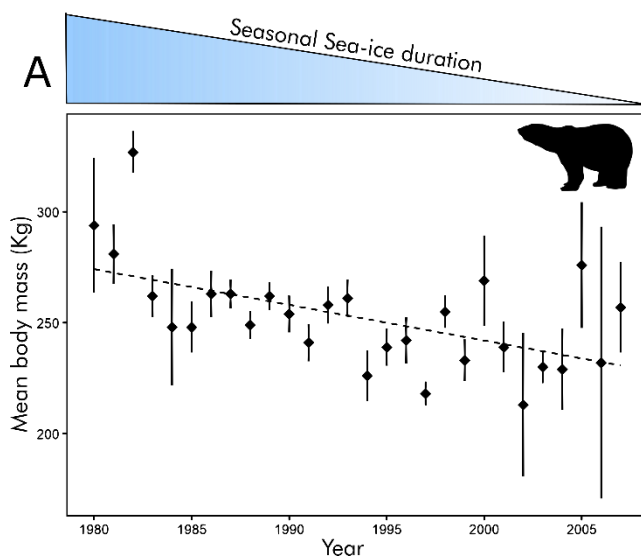
BOX 3. Timeline fragments

Whilst there are still no quantitatively documented examples of a complete timeline to collapse, we can find partial examples that lend empirical support in the literature (Box 3 Figure). For instance, a study on the Gulf of St. Lawrence's (Québec, Canada) humpback whale population found a shift in diet (i.e. behavioural change, Box 3 Figure A) caused by a decrease in resources[124]; years later, another study on the same population showed a subsequent decline in calving rates (e.g. life history adjustment, Box 3 Figure A). The authors postulated that this signal could indicate that the population trends can be affected in the near future by the environmental change[125], i.e. possibly entering the EWS phase of the timeline. Similarly, climatic change has impacted many polar bear populations through reductions in the extent of sea-ice. A study in a population in the southern Beaufort Sea of Alaska found first a body condition reduction (i.e. a morphological signal) and subsequently a decrease of reproductive rates and cubs survival[126] (Box 3 Figure B). The authors hypothesized that the short duration of the sea-ice platforms used for hunting induced a change in the feeding activity of the bears that triggered the loss of condition. Such a change in behaviour, although postulated, was not monitored for this population, otherwise this could have represented an almost complete example of the timeline to collapse concept. In fact, the abundance of the same population was monitored in a more recent paper that found a slight decrease compared to previous years estimates[127]. Such decrease indicate that the population might undergo an increasing abundance variability phase, and could be prone to show EWS of collapse, if sea ice keeps reducing. Another example of partial timeline can be found in the work of Clements et al.[34] , where the authors analysed data on the historical collapse of, among others species, sperm whale populations due to over harvesting; the observed collapse in abundance was found to be preceded by a change in body size of individuals (likely due to the size selective whaling pressure), and subsequently EWS were detected before the decline (Box 3 Figure C). Similar patterns were found in a historical population of Atlantic cod that, during a fishing induced critical collapse in abundance, showed a concomitant change in morphology and life history (e.g. smaller size and earlier age at maturity[128]). Moreover, despite taxonomic difference in detection rates and warning times, EWS were observed several times in a large meta-analysis of global fisheries populations[129]. Finally, the population of the Bramble Cay melomys was declared extinct in 2016, after a continuous decline in the abundance estimates observed in scattered monitoring activities[130]. The oceanic inundation rate increase due to climate change is hypothesized to have driven a strong habitat and resources reduction responsible for

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822   the Bramble Cay melomys decline. It seems likely that some change in the movement patterns and in the

823   condition of individuals would have been observed before the ultimate collapse of this small rodent's popula-

824   tion. Despite the weight of evidence from these rich partial examples, a complete timeline to collapse has yet

825   to be observed, given the complexity of collecting such multivariate data on stressed populations. Nevertheless,

826   current technological advancements increasingly offer opportunities to collect such multivariate data in higher

827   resolution than have been previously possible[73] (see Supplementary Material Table S1).

828