Timeline to collapse

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Abstract

Contemporary rates of biodiversity decline emphasize the need for reliable ecological forecasting, but cur-rent methods vary in their ability to predict the declines of real-world populations. Acknowledging that stress acts at the individual level, and that it is the sum of these individual-level effects which drives popu-lations to collapse, shifts the focus of predictive ecology away from using predominantly abundance data. Doing so opens new opportunities to develop predictive frameworks which utilize increasingly available multi-dimensional data which have previously been overlooked for ecological forecasting. Using this ra-tional, we propose that stressed populations will exhibit a predictable sequence of detectable changes through time: (i) changes in individuals' behaviour will occur as the first sign of increasing stress, followed by (ii) changes in fitness related morphological traits, (iii) shifts in the dynamics (e.g. birth rates) of popu-lations, and finally (iv) abundance declines. We discuss how monitoring the sequential appearance of these signals supplies information to discern whether a population becoming increasingly stressed risks collapse or is adapting in the face of environmental change. Such a timeline of signals provides a new framework to implement forecasting methods combining multidimensional data (e.g. behaviour, morphology, abun-dance) that may increase the ability to predict population collapse.

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Abstract

Contemporary rates of biodiversity decline emphasize the need for reliable ecological forecasting, but current methods vary in their ability to predict the declines of real-world populations. Acknowledging that stress acts at the individual level, and that it is the sum of these individual-level effects which drives populations to collapse, shifts the focus of predictive ecology away from using predominantly abundance data. Doing so opens new opportunities to develop predictive frameworks which utilize increasingly available multi-dimensional data which have previously been overlooked for ecological forecasting. Using this rational, we propose that stressed populations will exhibit a predictable sequence of detectable changes through time: (i) changes in individuals' behaviour will occur as the first sign of increasing stress, followed by (ii) changes in fitness related morphological traits, (iii) shifts in the dynamics (e.g. birth rates) of populations, and finally (iv) abundance declines. We discuss how monitoring the sequential appearance of these signals supplies information to discern whether a population becoming increasingly stressed risks collapse or is adapting in the face of environmental change. Such a timeline of signals provides a new framework to implement forecasting methods combining multidimensional data (e.g. behaviour, morphology, abundance) that may increase the ability to predict population collapse.

INTRODUCTION

The extinction rates over the last century has been estimated to be higher than the historical background rate (e.g. up to 100 times higher for vertebrates), with human activity identified as the predominant driver of this "sixth mass extinction" (Ceballos *et al.* 2015). In addition to the positive effects of biodiversity on human wellbeing and culture (Dereniowska & Meinard 2021), such declines undermine the stability and resilience of ecological systems on which humanity relies for food, fresh water, and clean air (Maron *et al.* 2017). At the root of human induced extinctions are a suite of stressors - including habitat loss, pollution, overharvesting, and climatic change (Tilman*et al.* 2017) - which can drive declines and erode a population's ability to recover in the face of disturbances, increasing the probability of rapid collapses in the abundance of the populations (van de Leemput *et al.* 2018). Indeed, anthropogenic pressure often creates scenarios where negative biotic and abiotic stressors mutually reinforce one another and affect, through a domino effect, multiple facets of populations, driving it precipitously to extinction – the so called extinction vortex (Fagan & Holmes 2005; Williams *et al.*2021). 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 (Clements & Ozgul 2018).

This need has driven the development of numerous predictive methods that aim to forecast the risk of population collapse, ranging from classical Population Viability Analyses (PVA, Shaffer 1991) to more recently developed Early Warning Signals (EWSs, Clements & Ozgul 2018). However, the difficultly of surveying wild populations, together with economic limitations (Gardner *et al.* 2008), often results in noisy and short abundance time series data which can detrimentally affect the accuracy of predictive frameworks such as the EWSs (Clements et al. 2015). Moreover, this approach has neglected other potentially powerful diagnostic features which theory and evidence suggest should be impacted by increasing stress, and thus could act as additional indicators of increasing extinction risk. Indeed, the decline of a population to extinction is a manifestation of a host of changes to the structure and dynamics of that population. Such changes occur first at the individual level (e.g. decline in the body condition of an individual) which, when a high enough proportion of the population exhibit similar changes of sufficiently high magnitude, affects the dynamics of that population. Therefore, additional signatures of approaching collapse could include changes in the behaviour of individuals (Berger-Tal *et al.* 2011), and value of morphological traits (Baruah *et al.* 2019), alongside traditional abundance-based measures of extinction risk (Clements & Ozgul 2018). At the individual level, many behaviours and morphological traits have a range of plasticity to maintain fitness in the presence of environmental variability and stress (Fox *et al.* 2019); however, if conditions continue to change, this adaptive plasticity may not be enough to maintain reproductive capacity and survival of individuals (i.e. fitness), eventually affecting population abundance.

Thus, the effect of increasing stress on a population propagates from the individual level to the population level via a successive series of reactions (or "signals of stress") through time. Such individual level responses necessarily take place (and are observable) over smaller time scales compared to population level signals; an individuals' behaviour or morphology can change during their lifespan, while the effect of stress at the population dynamics (e.g. decreases in abundance) will happen after one or more generations. Incorporating this individual-to-population concept offers not only the opportunity to use individual responses to stress as early indicators of change in population conditions, but to measure the impacts of this stress on multiple-dimensions simultaneously. Such an approach expands on recent work in the field of EWSs, where abundance based EWSs and shifts in the mean body size of the population are considered concurrently, leading to an increase of the overall predictive power (Clements & Ozgul 2016; Clements et al. 2017). These results suggested that integrating multi-dimensional data to predict population collapse has significant merit, whereby signals of stress from a range of ecological disciplines may be combined to increase the reliability of warning signals, decrease the length of the time series required to generate such signals, and increase the time prior to collapse in which signals are detectable.

Here we develop a conceptual framework – the "timeline to collapse" – supported by case studies, where we: i) describe how increasing environmental stress shapes different features of individuals across time, ii) state the temporal sequence of observable stress signals from individual to population level along the path to extinction, iii) show how this "timeline" of responses provides a signature to corroborate whether a population is at risk of collapse and iv) outline methods to gather the data needed to implement such an approach. Additionally, we will explore how the timeline provide information on individuals and population stress buffering capacities. The feasibility of this framework relies on organisms showing measurable behavioural plasticity, and thus within this review we will primarily consider animals as examples and case studies, but where applicable we will highlight concepts that are relevant to non-animal species. Henceforth, we will refer to "environmental stress" - or more in general to "stress" - as the presence of biotic and/or abiotic factors (e.g. resource scarcity, pollution, invasive species etc.) that effects a population in a negative way. In the following sections we will consider responses to stress observable over the short term (rapid changes;<<1 generation), medium term (intermediate speed changes; [?]1 generation) and long term (slow changes; >1 generation).

RAPID CHANGES

Behavioural changes are amongst the most rapid changes that individuals can perform to cope with sub-optimal conditions (Greggor *et al.*2016). The potential range of behaviours individuals can present in the face of stress is a result of evolved mechanisms that shape strategies to maximize fitness, intrinsic plasticity and the past experiences of the individual (Tuomainen & Candolin 2011). Broadly, such behaviours comprehend those related to movement and habitat use, foraging activities, and reproductive and social behaviours (Berger-Tal *et al.* 2011). That different categories of behaviour can be modified by stress is well documented, with many studies showing variation in e.g. foraging activity and dispersal of individuals in response to declining resource availability (Couvillon *et al.* 2014; Fayet *et al.*2021), climatic change (Hamilton *et al.* 2015; Holt & Jørgensen 2015; Gauzens *et al.* 2021), and invasive species (Lenda *et al.* 2013). Indeed, changes in the movement patterns, speed, and position of individuals in their environment can be amongst the first signals to manifest in response to increasing environmental stress, as individuals seek to minimise the impacts of, say, declining food availability by moving to new foraging areas (e.g., increased foraging effort, Figure 1A) or by reducing activity levels (depressing metabolism, Trites & Donnelly 2003). Such changes constitute some of the most easily observed and measurable behavioural signals of increasing stress, as they can often be captured remotely through e.g. GPS tracking or remote camera monitoring, techniques which bridge taxa (vertebrate and invertebrates, Hertel *et al.* 2019, Tini *et al.* 2018) and realms (marine and terrestrial , Shimada *et al.*2021).

In addition to movement patterns, individuals may react to stress by altering rates of intra-and -interspecific interactions, with effects observed also in social and communicative behaviours (Kunc & Schmidt 2021). For instance, resource scarcity may lead individuals to prefer energy allocation in essential activities (e.g. foraging), decreasing actions not linked to strict survival such as the engagement in territorial defense (e.g. in coral fishes, Keith *et al.* 2018, Figure 1B). Similarly, acoustically active insects and amphibians may change the acoustic properties of the mating signals in response to temperature stress (e.g. crickets call speed increase at high temperature, Singh*et al.* 2020). Moreover, human disturbance (e.g. presence of boats) can induce reductions in whistles and echolocation click rates of social cetaceans (Pellegrini *et al.* 2021).

Increases or decreases in behavioural metrics (foraging distance, prevalence of an interaction type, duration in time of given actions etc.) will vary depending on species environmental tolerance, trophic level (e.g. prey vs predator) and stressor type. Whilst a lack of resources may trigger increases in movement, the arrival of an invasive predator in an ecosystem may induce a prey species to reduce movement (to reduce encounter rates) or to shift microhabitat use toward a more shelter-oriented strategy (i.e. less time spent in open areas, McMahan & Grabowski 2019). In addition to these directional changes, environmental stress may increase the variance observed while monitoring behavioural metrics, e.g. poor environmental conditions enhanced the variability of foraging trip duration in young albatrosses (Patrick*et al.* 2021).

Previous experience may also play a critical role in determining an individual's response to stress. Individuals that have previously faced similar situations may cope better with a novel stress if cues share similar characteristics to those already experienced. For instance, compared to naïve individuals, fishes with previous experience of predation events showed stronger antipredator behaviours (e.g. decreasing swimming activity) when they were represented with the chemical cues of the predator (Vilhunen *et al.* 2005). Likewise, the evolutionary history of a population can shape an individuals' capacity to react to environmental pressure. A lizard prey species will likely recognize a new predatory snake introduced in its habitat as dangerous and perform antipredatory behaviours if the lizard's population have evolved with other snake species, especially if the predators share similar features (shape, chemical cues etc.) with the introduced predator (Ortega *et al.* 2017). On the other hand, lizards that have never seen predatory snake in their evolutionary past (e.g. due to geographical isolation, (Durand *et al.* 2012)) are less likely to recognize an alien snake as dangerous, and thus may suffer heavy predation (i.e. lack of antipredatory response). (Sih 2013; McMahan & Grabowski 2019). Consequently, a population's ecological and biogeographical history must be considered when looking for such behavioural signals of stress.

Such changes in individual's behaviour can occur over short ($<<$ 1 generation) timescales, as such shifts are driven by physiological needs and immediate adaptative reactions which take place rapidly. For instance, the micro-habitat use shift by an insect prey can happen overnight after a predator arrival (Pierce 1988); similarly, an increase in movement of individuals due to food scarcity can be triggered after months, days, or hours depending on the species life span and metabolism speed. Regardless, such fast behavioural changes represent an individuals' primary stress buffering response, and consequently will manifest as the first of the suite of detectable warning signals.

INTERMEDIATE SPEED CHANGES

If rapid behavioural plasticity is not enough to mitigate the effects of increasing stress, individuals may respond to maximize survival and reproductive output through changes in morphological traits related to fitness (Fox *et al.* 2019). Such changes can include metabolic adjustments (e.g. reductions in body mass, decreases in growth rate) as well as antipredatory morphological trait expression, and their plasticity shapes an individual's capacity to respond to rapid environmental change (Fox *et al.* 2019), thus governing the vulnerability of populations to extinction (Olden *et al.* 2007).

Environmental stress substantially affects morphological trait distributions, both prior to or concurrent with changes in the demography of the population (Pigeon *et al.* 2017; Baruah *et al.* 2019). For instance, the reduction in body size of populations due to sub-optimal food consumption is a general response to resources scarcity (Trites & Donnelly 2003). Reductions in body size are also directly and indirectly induced by climatic change and habitat fragmentation, with such shifts being observed across numerous taxa (Lomolino & Perault 2007; Gardner *et al.* 2011; Sheridan & Bickford 2011; Stirling & Derocher 2012; Thoral *et al.* 2021, Figure 2A). Indeed, body size is a key trait that directly affects thermoregulation dynamics and rates of energy and mass intake and utilization (Gardner *et al.* 2011), and has recently been suggested as a possible measure of population stability (Clements & Ozgul 2016). For example, changes in body size of diatoms algae preceded a regime shift in a lake ecosystem (Spanbauer *et al.* 2016), and experimental populations exhibit the same pattern, showing that – when resources decrease – declines in average body size precede declines in population size, and hence could be indicative of a future population collapse (Baruah *et al.* 2019).

In situations where measuring body size changes is inappropriate, change in individual growth rates can be used as an even more accurate stress signal since growth rate will respond instantaneously to physiological adjustments made by the individual in response to stress. For example, Bjorndal *et al.* 2017 reported a decrease in growth rate of individuals of three sea turtle species in response to climatic stressors and anthropogenic degradation of their foraging areas. Similarly, environmental stress can lead to a decrease in defensive morphological traits: e.g. light stress in pregnant individuals of a freshwater cladoceran crustacean induced the reduction of antipredator spines dimensions in their offspring, with a consequent enhancement of the predation risk for newborn individuals (Eshun-Wilson *et al.*2020).

Even if such reductions in the size of morphological traits are the most likely outcome of stress, particular stressors may result in other patterns of change. For instance, the novel pressure that an invasive predator species brings on a native population can trigger the increasing of body features (predator induced-defenses , Zhang *et al.* 2017)) aimed to better escape negative interactions (attack/predation), if the alien predator is perceived (via visual or chemical cues) as a threat (Thawley *et al.* 2019). Moreover, chemical pollution has been found to increase the occurrence of fluctuating asymmetry in body traits linked to intraspecific interaction (i.e. femoral pores, Figure 2B) in lacertids (Simbula *et al.*2021). Indeed, increase in fluctuating asymmetry has been suggested as an indicator of the loss of genetic variation possibly occurring prior to extinction (Leary & Allendorf 1989).

These physiological responses, including (but not limited to) declining body mass/size, expression of chemical induced antipredatory features, and asymmetry in meristic features will generally occur over longer time periods than rapid behavioural changes described above, but may still occur within the life span of an individual (i.e. [?]1 generation), or be tracked across multiple sequential generations (e.g. Clements & Ozgul 2016; Clements *et al.* 2017). For instance, the body size reductions induced by food scarcity can be observed both during an individual's life and across generations (e.g., seabird annual breeding season (Fayet *et al.* 2021)), as the nutrient deficit of the parents is reflected by loss of condition in the hatchlings. Likewise, toxic chemicals can accumulate in adult females inhabiting polluted habitats and be transferred to their eggs, and the induced traits shift could appear in the offspring over a single reproductive season (e.g. few months for lizards, Simbula *et al.* 2021). Therefore, after behavioural changes, morphological trait shifts represent the next viable response to stress (i.e., second buffering level) of individuals, and should thus occur as the second indicator of increasing stress on a population.

SLOW CHANGES

The signals discussed thus far represent the impacts of stress observable at the individual level; however, when a high proportion of a population is similarly stressed, such individual level effects can propagate to alter the structure and dynamics of a population through changes in births, deaths, immigration, and emigration. Examples of fitness related phenotypic changes that shape an individual's life history traits (e.g. shift in fecundity (Boggs & Ross 1993)) and thus population dynamics are numerous in the literature. For example, climatic change impacted the feeding activity of many polar bear populations, resulting first in body condition reductions and subsequently in a decreases of reproductive rates and cubs survival (Stirling & Derocher 2012). Similarly, behavioural plasticity can impact population dynamics in the long term: a recent example in humpback whales has shown that changes in behaviour (shifts in diet and seasonal movement) driven by environmental change led to a subsequent decline in calving rates (Kershaw *et al.* 2021). Such decreases, which necessarily reduce the lifetime reproductive success of an individual, represent some of the the last stages of adaptive plasticity in life history, where resources are reallocated from reproduction to maintain the survival of the individual whilst allowing for the possible exploitation of improved future conditions (Fleming *et al.* 2016). Although such responses are carried out by the individuals during their lifetime, i.e. occurring right after to or concurring with the morphological shifts, the resulting signals become observable over long (>1 generation) time frames via changes in the abundance trends of a population. Indeed, such decreases in reproductive success and increases in mortality will drive fluctuations significantly different from the preceding stable periods (e.g., increasing variance EWS (Clements & Ozgul 2018)). However, these changes will not necessarily trigger/drive continuous declines in the abundance until extinction (i.e. the population could stabilize at a new carrying capacity level with lower resources quantity).

These slowly occurring changes represents the ultimate signals (last stress buffering level) a population may show before the collapse starts. Indeed, such a state of low recruitment potential may be critical as the plasticity of behaviours and body traits may have already been exhausted, and thus a population is more vulnerable to fluctuations and collapse if stress continues to increase, or through stochastic factors (e.g., catastrophic events). At this point, if stress – be that abiotic or biotic – continues to increase then even this last stress buffering level of the population will be overcome, death rate will increase, and abundance will start to continuously drop until the ultimate extinction of the population.

THE TIMELINE TO COLLAPSE

The above changes – ranging from rapid behavioral responses to declines in the abundance of a population – constitute a predictable succession of observable signals which we term the "timeline to collapse" (Figure 3). The presence of these signals assumes a continuous increase in stress – be that biotic or abiotic – such that a population is able to respond, rather than sudden step-shifts in a stressor which may eradicate a population in the absence of any indicators (Clements & Ozgul 2018).

Whilst the time at which behavioral, morphological, and abundances shifts start (T_{Bs}, T_{Ms} and T_{As}, Figure 3) are expected to be sequential, the time intervals over which such shifts occur (I_B, I_M and $I_{A,}$ Figure 3) may overlap. Indeed, for an organism, changing a behaviour above a given threshold may require the use of energy reserves that may trigger a change in morphological traits. For example, for a seabird population (Figure 3), increasing foraging distance may be the first response to decreasing food availability, and in normal conditions the resources found in a further area may be enough to compensate this additional foraging effort; but if the food is needed for recruitment (i.e. feeding chicks, (Fayet *et al.* 2021)) most of these resources will be transferred to the offspring, and may not cover the individual's energy cost of increasing flight distance. Therefore, an individual will either i) fail to replenish energy stores (e.g. start to lose weight) or ii) decrease feeding rate to offspring to ensure they have the energy needed to cope with the extended foraging distance (Fayet *et al.* 2021). This will result in observing flight distance increasing together with declines in the body weight of adults, offspring, or both. However, in other scenarios we could observe a clear temporal distinction between signals of stress time (i.e. no overlap among I_B, I_M and I_A). For instance, in the presence of an invasive predator a prey species can go through an initial fast and discrete behavioural change (e.g., a shift in microhabitat use (Pierce 1988)), followed by a medium speed response (e.g., change in body size due to different conditions in the new microhabitat, (Leibold & Tessier 1991)), without any overlap between these two signals.

The timeline can act as novel tool to discriminate populations tending toward extinction from those simply adapting in the face of change. For instance, focus on a single feature such as behaviour cannot discern a population where individuals' behavioural shifts are sufficient to cope with stress (maintain fitness) from a population where individuals reach the maximum level of behavioural plasticity and then start to compensate the fitness loss with changes in morphological traits (e.g. decrease in body size). In both cases, the monitoring would demonstrate a significant change in behaviour. Instead, observing the temporal sequence of changes in all the facets (behaviour, morphological traits, changes in the variances of abundance, and finally abundance declines) represent the key indicator that the stress gradually overcomes individual and population level reactions, and thus collapse is approaching.

These temporal pattern in signals of stress will necessarily be across time scales relevant to the study organism, i.e. lifespans and generations rather than absolute time periods. For small invertebrates, fast response that may be observable over hours (e.g., *Daphnia*depth shift, Oram & Spitze 2013) while slow signals will occur over days. For larger vertebrates, medium speed response may take place over months (e.g., Steller sea lions weight loss, Trites & Donnelly 2003) whilst EWSs occurrence and subsequent abundance declines may occur over years. Regardless of the direction of the shifts and the stress type, we expect the temporal sequence in the typology of signals (behavioural, morphological, abundance; Figure 3) to remain broadly consistent.

Data requirements

The conceptual development of the timeline to collapse offers hope that multiple data streams can be synthesized into a single predictive tool which incorporates both the timing of changes in signals of stress, and the order in which such signals occur. To apply such a framework to at risk populations would require simultaneous monitoring of the behaviour, morphological and/or life history traits, and abundance of populations. Whilst such multivariate data may seem challenging to gather in real world situations, recent technological advancements in data-collection methods provide the opportunity to generate high throughput information on these multiple features of populations with a relatively low cost/benefit ratio (Thompson 2013; Ward *et al.* 2017). Indeed, GPS tracking, biologging, acoustic monitoring, and photographic analysis are now able to extract data on behaviours and morphological traits, providing invaluable data even from a subset of the population, (Desjonqueres *et al.* 2020; Williams *et al.* 2020; Sequeira*et al.* 2021; Shimada *et al.* 2021), and such approaches have been implemented in vertebrates (both terrestrial and marine) and invertebrates (Table 1). Biologging sensor are becoming rapidly more affordable, and research to reduce the relative mass of these devices ameliorates the ethical implications of weight and invasiveness (Portugal & White 2018). Current biologger models can already collect, among other information, data on geographical location, body movement (e.g. posture, rotation, heading), physiological rates (e.g. heartbeat, temperature, reproductive periods) and acoustic data (e.g. vocalizations, external soundscape), widening the possibilities to observe behavioural stress responses simultaneously in several aspects of the individuals' life (Table 1, Williams *et al.* 2020). Similarly, for sound-emitting species, passive acoustic monitoring allows the assessment of individuals' behaviour, health status, distribution, and population dynamics (Gibb *et al.* 2019; Desjonqueres *et al.* 2020). Acoustic sensors (microphones and hydrophones) are relatively easy to deploy, can be used in low visibility environments such as dense forests or deep-water and be left*in situ* for long times, and have the advantage of being non-invasive and able to survey a broad taxonomic range spanning from vertebrates (e.g., cetaceans Sousa-Lima *et al.* 2018; bats, Tuneu-Corral *et al.* 2020; birds and amphibians, Deichmann*et al.* 2017; Table 1) to insects (e.g. Orthopterans (Singh et al. 2020)). Moreover, unmanned aircraft systems (e.g. drones) now allow to perform precise photogrammetric measurements of species that are challenging to sample: drones photography can take measurements of big marine mammals like pinnipeds and whales (also good ecosystem health indicators, Krause *et al.* 2017; Kershaw *et al.* 2021)) and estimate their mass and body condition, thus providing data on possible shifts in body size (Clements *et al.* 2018).

Similarly, abundance estimates are being improved through new tools and statistical models that complement classic approaches like direct sampling and capture-mark-recapture methods (Seber & Schofield 2019). Camera traps, and aerial and satellite images can be analyzed with machine learning techniques to obtain accurate population counts even for multiple species systems (Linchant *et al.* 2015; Norouzzadeh*et al.* 2018), and citizen science projects can help to gather and process such image data (e.g. *Penguin Watch* (Jones *et al.*2020)). Moreover, the recent explosion in environmental DNA (eDNA) analyses can provide a cost-effective way to estimate populations that is applicable to a large number of systems and taxa (Yates *et al.*2019). This broad suite of cutting-edge methodologies means that data on multiple facets of a population will become increasingly available, much of which has been largely overlooked by predictive ecology but which can be leveraged under the timeline to collapse framework.

Forecasting

The timeline to collapse provides a conceptual framework to synthesize multiple types of data to aid predicting the future dynamics of ecological systems (Clements & Ozgul 2016). However, to apply the timeline to collapse concept requires identifying appropriate data to monitor (behaviours, traits), measuring baselines against which change can be quantified, developing statistical tools to provide robust detections of increasing stress.

Whilst some behaviours and morphological signals may provide general indicators of increasing stress (e.g. increased dispersal), selecting signals which are relevant to the taxa of interest remains key (McClanahan *et al.* 2020). Expert knowledge can aid in this (Reside *et al.* 2019), identifying which behaviours and traits are most likely to change given the nature of the stressor, or – in cases when the identity of the stress is unknown – what can provide general indicators of an individual's condition. After choosing what to monitor, a quantitative and/or qualitative definition of "normal" values for the identified behavioural, morphological, and abundance indicators is needed, from which we expect to observe significant deviations when environmental stress starts to increase (Figure 3). Defining such values in wild populations ideally requires long term monitoring data (Wauchope*et al.* 2021) on the multiple features of a population under stable conditions. Such data will become progressively more available as remote sensing and technological advancements continue to automate data collection at large scales (Krause *et al.* 2017; Sequeira *et al.* 2021). Alternatively, a comparative approach between populations experiencing different levels of stress can provide baseline values such as along a stress gradient (Ingram *et al.* 2021) – a so-called space-for-time substitution (Keith *et al.* 2018); Fayet et al. 2021). Such data on non-stressed populations can characterize the range of variation in the selected behaviours and morphological traits that, together with the abundance fluctuations, can be analyzed to obtain means and upper and lower confidence intervals. In the absence of such long-term monitoring data, methods such as Dynamic Energy Budget Models (DEMs) could help to set baselines using more general population life history data. DEMs describe in a single framework how individuals' energy is distributed for growth, somatic maintenance, development, maturity, and reproduction (Baas et al. 2018). Standard life-cycle data that can be obtained over shorter periods of time (e.g. Body length and weight at birth, growth rate, maximum reproduction rate, lifespan etc.) feed into the model that derive quantitative parameters describing the organisms energetics. Trait information can also be incorporated into the model to provide taxa specific estimates (Baas *et al.* 2018). Parameterizing such DEMs with life history data from populations in stable conditions could represent a viable and generalizable baseline distribution from which one can compare observed changes (Lika *et al.* 2011).

Regardless of how a baseline is defined, comparing these multivariate estimates to observed changes in behaviours, traits, and abundances is non-trivial. Recently developed statistical tools provide options to achieve this; multivariate time series modelling (Wei 2018) may offer a strong method for analyzing the timeline data (time series of behaviour, traits, and abundance), whereby the trends of the different variables can be analyzed through time while taking into account the inter-dependencies between them (e.g. behaviour and morphology). For example, Multivariate Autoregressive State Space (MARSS) models (Holmes*et al.* 2012) can use information on historical trajectories of multiple variables to forecast future values while accounting for multiple sources of uncertainty, and thus could represent another valuable option to predict shifts in, for example, behavioural indicators (Zhu *et al.* 2018). Alternatively, deep learning networks such as recurrent neural networks and temporal convolutional neural networks (Lai *et al.* 2018; Bury *et al.* 2021; Lara-Benitez *et al.* 2021) could provide an even more powerful approach to forecast future trends or state changes in such variables (Guo *et al.* 2020), though these tools will require large amounts of training data. Such approaches could be performed for single populations but may be stronger at the landscape scale, whereby one could combine inputs from multiple populations under different conditions and use the data to train the deep learning algorithms to then perform generic predictions in new cases. Therefore, despite the complexity of analyzing multivariate data, these new tools offer the opportunity to try to implement the timeline forecasting capacity.

Ecological insights

Whilst the temporal order of signals provides information on the population's future, the magnitude of the shifts in behavioural, morphological, and abundance-based metrics may provide measures of a populations ability to resist stress. For instance, for individuals of a population suffering from resource loss (Figure 4), increasing their foraging distance can initially compensate against the increased stressor levels' (i.e. buffering a given quantity of stress). However, above a threshold (Figure 4, Point 1), expanding such behaviour is insufficient to maintain fitness, and the animals' body size is impacted. Body size will also ultimately decrease if stress growth persists, until a physiological limit is encountered, beyond which the reproductive ability of a population is impacted (Figure 4, Point 2). Therefore, the variation from the average value of pre-stress (stable) conditions, measured in the behaviour and morphological trait prior the onset of the next signal of stress, represents an intrinsic stress buffering capacity (C): a measure of the magnitude of stress tolerable before transitioning to the subsequent stress buffering level along the timeline. If we define $\mathrm{B_s}$ and $\mathrm{M_s}$ as the average values of a monitored behavioural metric and morphological trait during stable conditions, and $\mathrm{B_x}$ and $\mathrm{M_x}$their respective values at the onset of the next buffering signal/level (Figure 4, Point 1 and 2), we may calculate $\mathrm{C_b}$(behaviour C) and $\mathrm{C_m}$ (morphological trait C) as follows:

$\mathrm{C_b}=|\mathrm{B_s} - \mathrm{B_x}|$; $\mathrm{C_m}=|\mathrm{M_s} - \mathrm{M_x}|$.

From this framework, average values of $\mathrm{C_b}$ and $\mathrm{C_m}$ of individuals can thus be calculated for particular behaviours or traits that can undergo continuous shifts and compared among different species and populations. For instance, nematodes and rotifers show extreme plasticity in morphology (reduction of up to one-thirds of original body size (Rebecchi et al. 2020)) to cope with long periods of stress (e.g. exsiccation of habitat), and thus they would display higher values of $\mathrm{C_m}$ compared to e.g. amphibians species with limited drought resistance. Such high value of $\mathrm{C_m}$ reflects the large amount of stress they can buffer by changing morphology before the eventual occurrence of abundance EWSs in the population. Therefore, such buffering capacities may be compared among different species to indicate which life history traits (group living vs solitary animals, bigger vs smaller dimensions, specialist vs generalist etc.) lead to species more resistant to stress. Additionally, average $\mathrm{C_b}$ and $\mathrm{C_m}$ may vary among populations of the same species, due to difference in biogeographic history and genetic structure (e.g. allelic heterozygosity (Hansson & Westerberg 2002)), which may provide information on how such factors shape stress buffering capacity.

Caveats

The timeline to collapse concept necessarily makes assumptions about how stressors will impact populations. The main assumption is that stressors will increase over time (Figure 4), allowing populations to respond gradually to increases in stress. However, as with EWSs and PVA, sudden and/or catastrophic stress (drought, storms, fires etc.) may lead to significant changes in the abundance or distribution of a population without any warning. Moreover, even in cases where stress increases continuously, 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, or concomitant abundance and trait change (Burant *et al.* 2021). Finally, whilst it is possible to apply parts of the timeline concept (and indeed doing so has been shown to improve the predictive accuracy of forecasting tools (Clements & Ozgul 2016, 2018)), applying the entire framework requires studying species that show quantifiable behaviours and morphological traits, where gathering data is easier at the individual perspective, and thus it may not be fully applicable to animals such as sessile (e.g. Anthozoa), obligate parasite species or to plants and fungi species. Nevertheless, we believe that in such cases a partial application of the timeline concept (e.g., monitoring morphological traits and abundance data) will improve the predictive horizon of eventual collapses compared to considering only one type of data.

CONCLUSIONS

Considering how anthropogenic stressors impact populations via changes in individual-level features provides a key step forward in predicting populations extinction. Doing so allows us to develop a conceptual framework, the timeline to collapse, where the temporal aspect of signals of stress can act as an additional corroborative tool to infer risk of population collapse. The timeline to collapse approach also provides a framework for the development of monitoring programs, highlighting what data might be collected to help enhance biodiversity monitoring, and how technological innovation might help to increase the amount of data available (Pimm et al. 2015, Table 1). A holistic view of how the behaviours, morphological features, and dynamics of populations change as they become increasingly stressed will improve the identification of what observable signals precede declines in the abundance of populations, thus strengthening the tool arsenal for fighting biodiversity loss.

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Table1 . Overview on data acquisition methods usable to collect the signals of the timeline to collapse.

Method	**Tools**	**Species**	**Signal category**	**Information**	**Ref.**
GPS tracking/bio-logging	GPS-GSM neck collars	*Ursus arcto*s	Behaviour	range of movement, diel activity, habitat selection	(Hertel *et al.* 2019)

Method	Tools	Species	Signal category	Information	Ref.
	GPS collars with integrated 3D accelerometer sensors + vaginal implant transmitters + machine learning techniques	*Ovibos moschatus*	Behaviour + morphological and life history traits	movements, energy allocation patterns, parturition events and body temperature	(Chimienti *et al.* 2021)
	GPS-GSM tags	*Halichoerus grypus*	Behaviour	Horizontal movement and diving behaviours	(Carter *et al.* 2017)
	GPS-UHF biologgers	*Falco naumanni*	Behaviour	Movement speed, distance, and duration.	(Lopez-Ricaurte *et al.* 2021)
Radio-telemetry	Radio transmitters	*Lucanus cervus*	Behaviour	Dispersal ability and space use	(Tini *et al.* 2018)
Passive acoustic monitoring	Hydrophones + Click Detector modules	*Physeter macrocephalus*	Behaviour	Seasonal occupancy, diel activity,	(Miller & Miller 2018)
	Microphones + Spatially Explicit Capture–Recapture models	*Arthroleptella lightfooti.*	Abundance	Population estimates (density)	(Measey *et al.* 2017)
Camera traps	Motion-sensor camera Trap + deep neural network learning	Multiple species	Behaviour + abundance	Identification of species, counts, behaviours	(Norouzzadeh *et al.* 2018)
Drones	Aerial photographs	*Megaptera novaeangliae*	Morphological traits	Body condition (photogrammetric measurements)	(Christiansen *et al.* 2016)
	Aerial photographs	*Hydrurga leptonyx*	Morphological traits	Mass and body condition (photogrammetric measurements).	(Krause *et al.* 2017)
	Aerial photographs	*Sterna hirundo*	Abundance	Population estimates (n individuals)	(Chabot *et al.* 2015)

Method	Tools	Species	Signal category	Information	Ref.
Satellite imagery	GeoEye-1 satellite images + artificial neural network	Multiple species	Abundance	Population estimates (n individuals)	(Yang *et al.* 2014)

Figure captions:

Figure 1 . Examples of stress induced behavioural shifts. A) Mean values of dive duration and distance travelled of individuals of ringed seal (*Pusa hispida*) in Svalbard (Norway) before and after a significant decline in sea-ice extension, and thus in their habitat quality. Both behaviours showed significant increases in response to the stress. Bars indicate standard error. Data adapted from Hamilton et al. (2015). B) Probability of aggressive encounters between heterospecific and conspecific butterflyfishes (*Chetodon* spp.) calculated in 4 regions across the central Indo-Pacific, before and after a mass coral bleaching event in 2006 (reduction in food resources for the fishes). Both behaviours showed significant decreases. Data adapted from Keith et al. (2018). Bars are 95% confidence intervals. *Coral cover % change showed refers only to one of the four sites (Christmas Island site, Indian Ocean; 105.6° E, 10.4° S) for simplicity.

Figure 2 . Examples of stress induced shifts in morphological traits. A) Mean estimated body mass of female polar bear individuals (*Ursus maritimus*) in western Hudson Bay from 1980 through 2007 (dashed line indicates fit of linear regression [r=-0.549, p<0.01], bars indicate standard error); the area experienced progressively earlier dates of sea-ice breakup, that is a decline in duration of the favorite sea-ice habitat of polar bears. Data adapted from Stirling & Derocher 2012. B) Comparison of the mean of individual asymmetry index for femoral pores among Italian wall lizard (*Podarcis siculus*) sampled in hazelnut orchards with no history of pesticide use (control) vs orchards regularly treated with pesticides (treatment). The pollution stress induced an increase in the fluctuating asymmetry for femoral pores (bars indicate standard error). Data adapted from Simbula et al. 2021.

Figure 3. Theoretical example of a timeline to collapse. Here we posit a population of seabirds inhabiting an area where prey resources (e.g. fish stocks) begin a continuous decline (A). The curves in B and C represent average values of a behavioural (B) and morphological trait (C) calculated from a pool of individuals in the population through time. The red curve in D shows the abundance of the population. First a shift is observed in the behaviour (time point T_{Bs}), where the average foraging distance increases compared to the average measured during stable conditions B_s (B). The foraging distance will increase until it reaches a physiological limit (time point T_{Be}), defining the time interval where a continuous change is observable (I_B). After, or during such time, we will observe a decrease in average body size compared to that measured during stable conditions M_s (C), at time T_{Ms}. The body size will change until its physiological limit (T_{Me}), defining the time interval where such continuous change is observable (I_M). Later, the abundance trend of population will show alterations in the pre-decline indicators such as Early Warning Signals (EWSs), that will start to be observable at time point T_{As}, and will last until T_{Ae}, defining the time interval I_A. Subsequently, the continuous decreases to extinction (D) will begin at time point T_{Es}, and end will end with the extinction of the population T_{Ee}, lasting the time interval I_E. The first occurrence of the signals projected on the lower Time axes shows the sequence in the category of observable signals of stress starting at the individuals' level (B, C) and propagating to the population level (D).

Figure 4. Theoretical example of a timeline to collapse. The grey curve represents a continuous growth of a given environmental stress on the population. The blue and green curves represent average values of a behavioural and morphological trait calculated from a pool of individuals in the population. The red curve represents the number of individuals. B_s and M_s are respectively the average measure of the considered behavioural and morphological traits in stable conditions. The small black dotted lines project the starting

point of the shifts in morphological traits and abundance dynamics on the behaviour (point 1) and morphological trait (point 2) curves. Projected on the vertical axis, those points identify B_x and M_x: the values of behavioural and morphological metrics at the time of the onset of the next signal along the timeline. The interval of change (brackets) from the average values defines the intrinsic buffering capacities of behaviour (C_b,) and morphological traits (C_m).

Figures.

Figure 1.

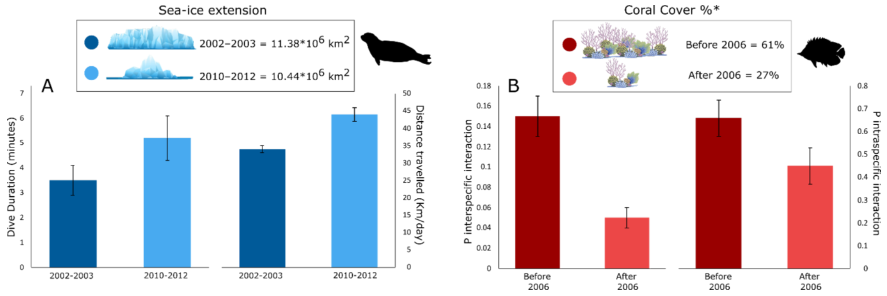


Figure 2.

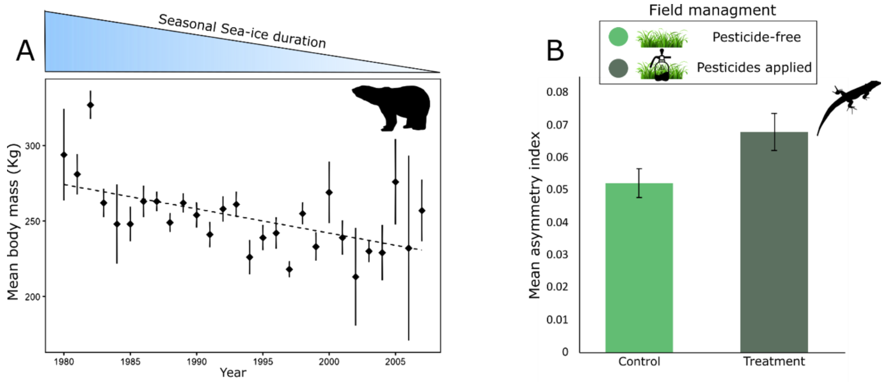


Figure 3.

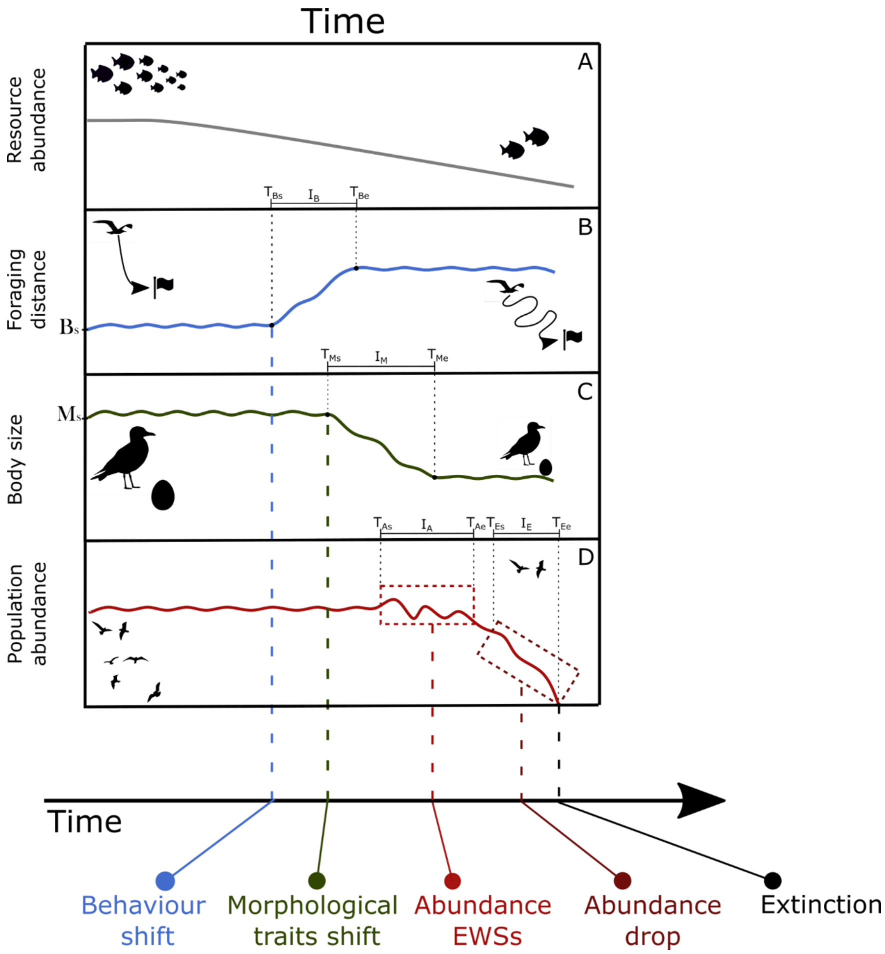
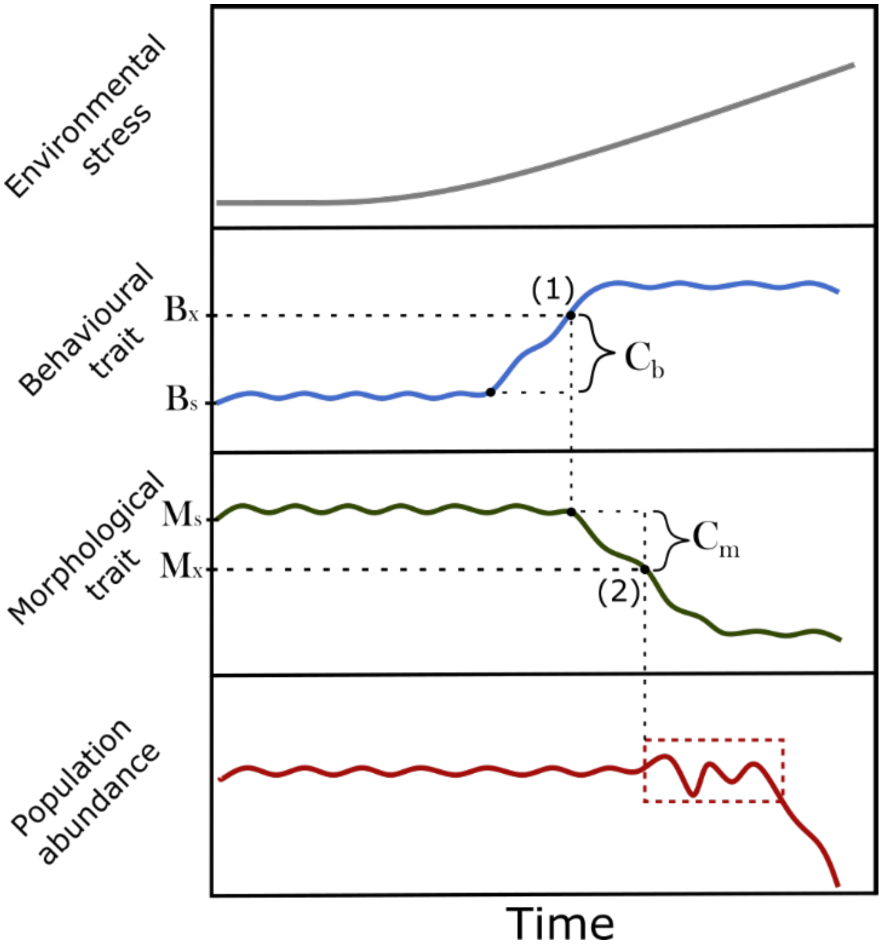

Time
Resource abundance
A
T_Bs
I_B
T_Be
Foraging distance
B
Bs
T_Ms
I_M
T_Me
Body size
C
Ms
T_As
I_A
T_Ae
T_Es
I_E
T_Ee
Population abundance
D
Time
Behaviour shift
Morphological traits shift
Abundance EWSs
Abundance drop
Extinction

Figure 4.


Environmental stress
Behavioural trait
Bx
Bs
(1)
Cb
Morphological trait
Ms
Mx
(2)
Cm
Population abundance
Time