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A geometric approach to understanding biological responses to environmental fluctuations from the perspective of marine organisms

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ABSTRACT: A main concern in marine ecology is understanding the mechanisms driving the responses of biological systems to environmental fluctuations. A major issue is that each biological system (e.g. organism, ecosystem) experiences fluctuations according to its own intrinsic characteristics. For instance, how an organism experiences a thermal fluctuation, i.e. as a long marine heatwave or as a mild pulse, depends on its thermal tolerance and developmental time, which can vary as the fluctuation is experienced. Here, a geometric approach is explored, considering the biological perspective. Environmental fluctuations are represented as points in a 'space of fluctuations'. The biological perspective is then defined as a coordinate frame within that space. Coordinates are given by components (e.g. amplitude and time scale) characterising each environmental fluctuation, which are then transformed into biological scales, using biological traits (tolerance and biological time). Using simulations of organisms growing under thermal fluctuations with different characteristics, the present study shows how this approach (1) enables the integration of physiology and phenology to better interpret biological responses to fluctuating environments; (2) improves our understanding of the role of adaptive plasticity as a rescue effect; and (3) facilitates our understanding of the effects of thermal fluctuations on additional organismal traits (e.g. body mass). Wider applications in the context of species persistence, coexistence, biodiversity and ecosystem function in scenarios of extreme fluctuations are also discussed.

KEY WORDS: Fluctuating environments · Marine heatwaves · Thermal tolerance · Phenotypic plasticity · Acclimation · Phenology · Multiple stressors

1. INTRODUCTION

One of the biggest challenges in marine ecology is understanding the mechanisms driving the responses of biological systems to environmental fluctuations (Thompson et al. 2013, Kroeker et al. 2020, Gerhard et al. 2023). Environmental fluctuations occur at several time scales (Chave 2013) and extreme fluctuations have increased over the past decades. For instance, marine and atmospheric heatwaves of periods ranging from days to months have become more frequent, more extreme, and less coherent in the past 30 yr (Russo et al. 2015, Hobday et al. 2016, Benedetti-Cecchi 2021). Ecologists are aware that fluctuating environments can drive biological systems through mechanisms that differ from those present in constant environments (Levins 1968, Sæther & Engen 2015, Denny 2019, Bernhardt et al. 2020). However, our mechanistic understanding of responses to environmental fluctuations is limited because most experiments use static designs, i.e. manipulating an environmental variable but keeping each treatment

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level constant over time. Results from experiments with static designs do not always produce accurate predictions of responses to fluctuating conditions. For instance, adaptive plasticity evolves strictly in fluctuating environments (Scheiner 2016); at the organismal level, adaptive plasticity may be triggered by a fluctuation after some environmental threshold is surpassed but not necessarily if the average condition of the fluctuation is experienced. Above a threshold, important (or irreversible) damage may lead to carry-over effects (Minuti et al. 2022). At the population and community levels, responses to mean conditions differ from those to extremes (Lynch et al. 2014). At the community level, fluctuations drive historical or legacy effects associated with the time scale of recovery time between fluctuations (Dal Bello et al. 2017). Storage effects and relative non-linearity are mechanisms sustaining species coexistence that operate strictly in fluctuating environments (Chesson 2018). Hence, in many cases, we cannot use the information provided by most static experiments even if they represent the average condition of the fluctuation.

Experiments are needed that manipulate the components characterising the fluctuations. Component fluctuations may be defined as the amplitude, average, maximum, minimum, time scale, and timing of a fluctuation (Jentsch et al. 2007, Gunderson et al. 2016, Donelson et al. 2018, Giménez et al. 2022). In the case of noise, such components may be defined as the intensity and the dominating frequency (Vasseur & Yodzis 2004), which have ecological and evolutionary consequences (Romero-Mujalli et al. 2021). Experiments provide mechanistic understanding (Benedetti-Cecchi 2003, Benedetti-Cecchi et al. 2006, Gunderson et al. 2016, Koussoroplis et al. 2017, Boyd et al. 2018, Gerhard et al. 2023) and are needed as a part of a wider set of methodologies (Dawson et al. 2011, Thompson et al. 2013, Koussoroplis et al. 2017). The experimental study of the effects of fluctuations on biological systems brings both logistical and conceptual challenges (Thompson et al. 2013, Giménez et al. 2021, 2022). Logistical challenges associated with the number of replications have been addressed through specific experimental designs (Boyd et al. 2018, Kreyling et al. 2018). Issues associated with teasing apart the role of different components characterising a fluctuation have also been addressed in the case of disturbance events, with intensive efforts being made to separate the effects of the mean and temporal variance of a fluctuation (Benedetti-Cecchi 2003, Benedetti-Cecchi et al. 2006, Bertocci et al. 2005, 2007, Maggi et al. 2012).

In recent years, there has been an intensive effort to generate a general framework to incorporate fluctuations into studies of the effects of climate change on organisms (Gunderson et al. 2016, Boyd et al. 2018, Gerhard et al. 2023). Within the framework, a major gap is the consideration of the organismal perspective (Jackson et al. 2021), given by how biological systems experience a fluctuation in relation to their own biological traits. The importance of studying the effects of environmental fluctuations on biological traits is obvious and has been widely recognised. We can, therefore, use current information on critical biological traits to develop a mathematical foundation and provide metrics to quantify fluctuation components from the organismal perspective. For instance, recent studies have quantified the time scales of thermal fluctuations using biological time as a trait (time to metamorphosis, Giménez et al. 2022; generation time, Munch et al. 2023). Some important facts (Fig. 1) motivating this approach are as follows. (1) Biological time scales such as generation time (or time to reproduction) are central traits with direct impacts on fitness (Stearns 1986 chapter 6, Angilletta 2009 chapter 6). (2) Adaptive responses, driving to evolutionary rescue (Chevin et al. 2010), can vary with time scales ranging from short-term plasticity (hardening) through acclimation to trans-generational plasticity and genetic adaptation (Gerken et al. 2015, Donelson et al. 2018). (3) In ectotherms, within species, increased temperature results in (i) strong non-linear effects on biological time through changes in metabolic rates (Gillooly, et al. 2002, Rombough 2003, Giménez 2011), (ii) increases in ageing rates (Burraco et al. 2020, Cayuela et al. 2021) and (iii) increases in the speed of behavioural responses (kinetic effects of temperature on behaviour; Abram et al. 2017). In ectotherms, the above changes are the result of increases in kinetic energy within cells and tissues; therefore, it is likely that changes in environmental temperature also affect the time scale of adaptive plastic responses. Studies of the effects of temperature on biological time have shown that (1) whether multiple-stressor responses are additive or interactive depends on whether time is measured in 'clock' vs. biological units (Giménez et al. 2022); this also extends to how sensitive organisms are to a given stressor; and (2) re-scaling the equations of population dynamics to biological time leads to more robust predictions of dynamics of ectotherms in seasonal environments (Munch et al. 2023).

Because of the nature of the fluctuations, we need a framework that considers biological time and additional traits as metrics of other fluctuation compo-

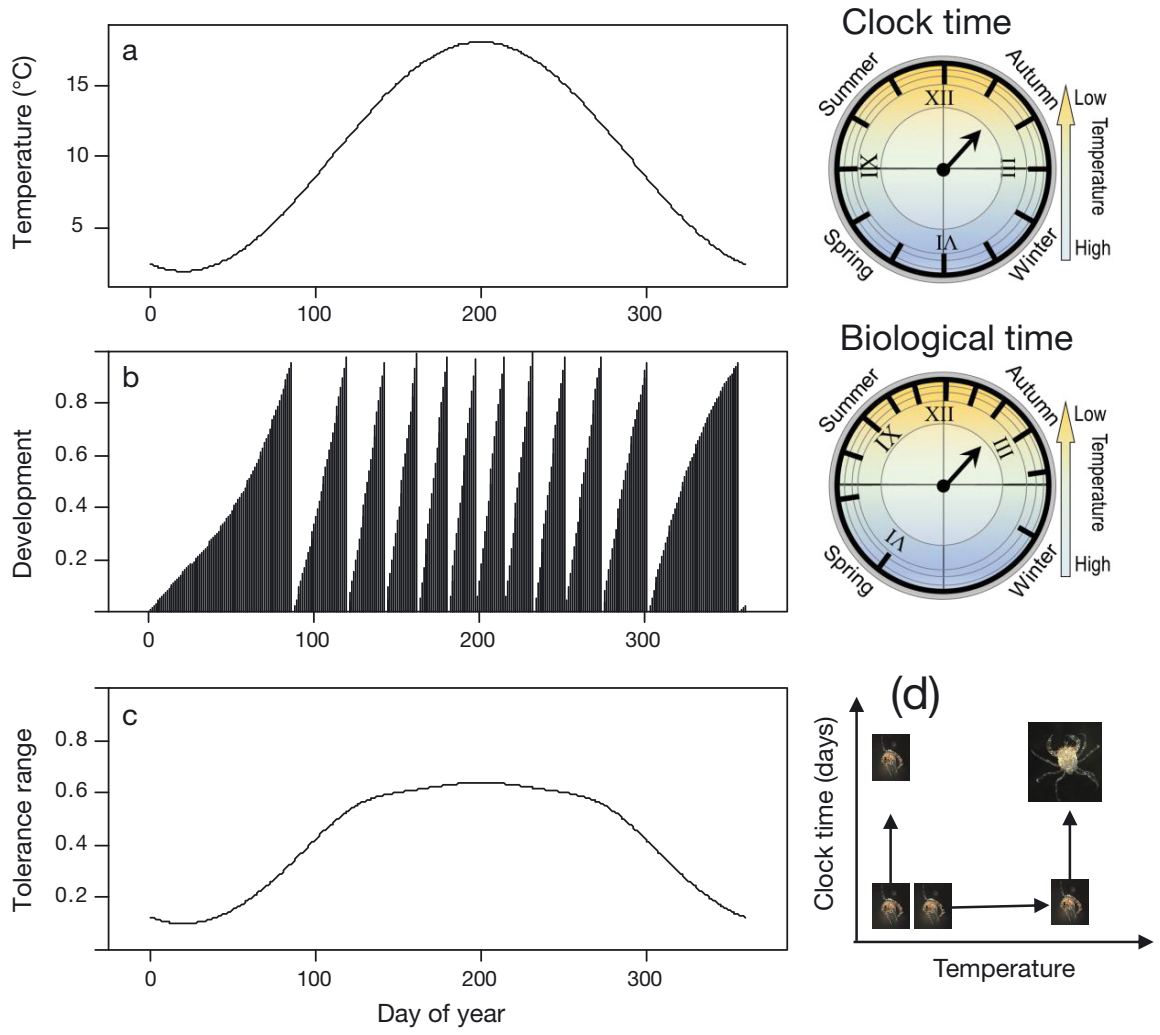

Fig. 1. Simulated example of responses to thermal fluctuations in a marine ectotherm developing through 12 stages. (a) A seasonal thermal fluctuation and associated clock time where each of the 12 divisions on the clock represents 1 mo and the colour gradient represents temperature (for simplicity, XII corresponds to the day of year of peak temperature). (b) Biological time: the cumulative proportion of development calculated as the proportion of development to each stage, using degree days (i.e. a stage is completed when the cumulative temperature reaches 280°C days). Once a stage is reached, the cumulative proportion resets to zero and increases until a new stage is reached. In the associated biological clock, the position of the stages varies depending on temperature. Hence, the division marks in the biological and clock time do not coincide. (c) Thermal fluctuation as experienced by the organism, calculated as the proportion of the upper thermal range (from the optimum to the upper thermal tolerance limit). The pattern of fluctuation is buffered relative to the pattern in (a) because organisms acclimate to high temperatures over the summer. (d) An experiment in which 2 sibling crab larvae are reared at different temperatures for a fixed amount of clock time, after which the sibling exposed to higher temperature is developmentally older than the one reared at low temperature. In (d), photographs by the author

nents. Hence, in the present study, I expand a previous framework, explored in Giménez et al. (2022), which did not consider a biological metric for the magnitude (e.g. intensity, amplitude, average) of an environmental fluctuation. A biological metric for fluctuation magnitude is critical, for example, to categorise a given fluctuation as an 'extreme event'. This is relevant in the context of, for instance, the study of heatwaves, where definitions may be based on climatology or biology (Bailey & van de Pol 2016) and on different references or baselines against which fluctuations are compared (e.g. Hobday et al. 2016, Jacox 2019). We also need to account for intra- and interspecific effects of environmental fluctuations and the associated mechanisms. Within a species, tolerance is shaped by both adaptive (i.e. adaptive plasticity and genetic evolution; Donelson et al. 2018) and non-adaptive responses (e.g. carry-over effects and 'silver spoon' maternal effects; Pechenik 2006, Uller et al. 2013, Ruiz-Herrera 2017). Mechanisms

underpinning tolerance also occur at other levels of organisation: populations may differ in their gene frequencies, which drive portfolio effects (Schindler et al. 2015, Šargač et al. 2022), and communities may differ in species composition, which drives species complementarity (Cadotte 2013), all acting as compensatory mechanisms. In those situations, tolerance should vary over time as a fluctuation is experienced. In synthesis, organismal experience (or that existing at other levels of organisation) can be quantified as tolerance and biological time, and this experience is characterised by complex dynamics which shape other biological responses.

The approach proposed here (based on the idea of a 'space of fluctuations': SOFiA) incorporates the perspective of the biological system in understanding biological responses to fluctuations. This is based on the idea (borrowed from differential geometry and physics; see e.g. Needham 2021) that there is no 'absolute' perspective to characterise a fluctuation and its components; instead, there are different perspectives from different systems (e.g. the human observer and an organism experiencing the fluctuation). The present study is structured as follows: first, SOFiA is presented in a wider context, aimed at making predictions of responses given field-observed environmental fluctuations. Second, the core ideas (space of fluctuations and coordinate frames to quantify the organismal perspective) are presented. Third, SOFiA is explored using 3 cases at the organismal level. Fourth, a worked example of a simulated factorial experiment is used, manipulating fluctuation components to clarify the design and data needed to quantify the organismal perspective. The emphasis is on the effects of thermal fluctuations at the organismal level; however, wider applications, on populations and ecosystems, are presented in Section 5.1.

2. METHOD CONTEXT

The approach proposed here must be viewed as being integrated into a wider framework (Fig. 2) combining field observations, experiments and models predicting the responses of biological systems to multiple fluctuating environmental drivers (Denny et al. 2009, Dawson et al. 2011, Koussoroplis et al. 2017, Gerhard et al. 2023). Thermal fluctuations (e.g. a heatwave) are characterised by a set of components, e.g. time scale, amplitude, cumulative intensity, and rates of increase and decrease in temperature (see e.g. Hobday et al. 2016 for marine heatwaves). Field observations provide information on the range of fluctuation types (characterised by their components) that are then used to define the range of values considered in an experiment. The effects of thermal fluctuations are quantified using factorial–orthogonal experiments, teasing apart the effect of each component. The output of the experiment can then be used for predictions in the field or for parameterization of models (Fig. 2). Predictions in the field may be based, for instance, on scale transition theory, a method that provides estimations of average responses from mean, variances and covariances of environmental variables (see worked example in Section 4.4) (Chesson 2012, Denny & Benedetti-Cecchi 2012, Dowd et al. 2015, Koussoroplis et al. 2017).

2.1. Experimental designs

The central point in SOFiA concerns the experimental phase: orthogonal experiments are necessary to derive quantitative relationships between predictors and responses and are essential for the development of mechanistic models (Benedetti-Cecchi 2003). This argument is also valid when different environmental variables (or fluctuation components) co-vary in the field. In such a case, the experiment will provide information that is relevant to the current environmental context, enable predictions of future scenarios where the covariation is broken (Benedetti-Cecchi 2003, Boyd et al. 2018) and cover for responses to rare events (Kreyling et al. 2014) such as extreme heatwaves. One may envisage an orthogonal experiment, considering fluctuation components as 'fixed' predictors (then analysed with e.g. ANOVA) or as continuous predictors. The latter method is more appropriate for the approach presented here, as it can be based on surface response designs (Box & Wilson 1951, Cottingham et al. 2005, Thompson et al. 2013, Kreyling et al. 2014, 2018, Schweiger et al. 2016).

Surface response designs will capture non-linear and non-additive responses to the fluctuation components present in the data. Because those responses are common in ecology and evolution (Levins 1968, Ruel & Ayres 1999, Scheffer 2009, Gunderson et al. 2016, Kroeker et al. 2020), surface response designs are better suited to improve ecological models than the ANOVA-type design (except when the predictor in question is categorical). Surface response designs also provide the appropriate response function needed in scale transition theory, developed to incorporate interactive and non-linear responses to environmental fluctuations (Koussoroplis et al. 2017).

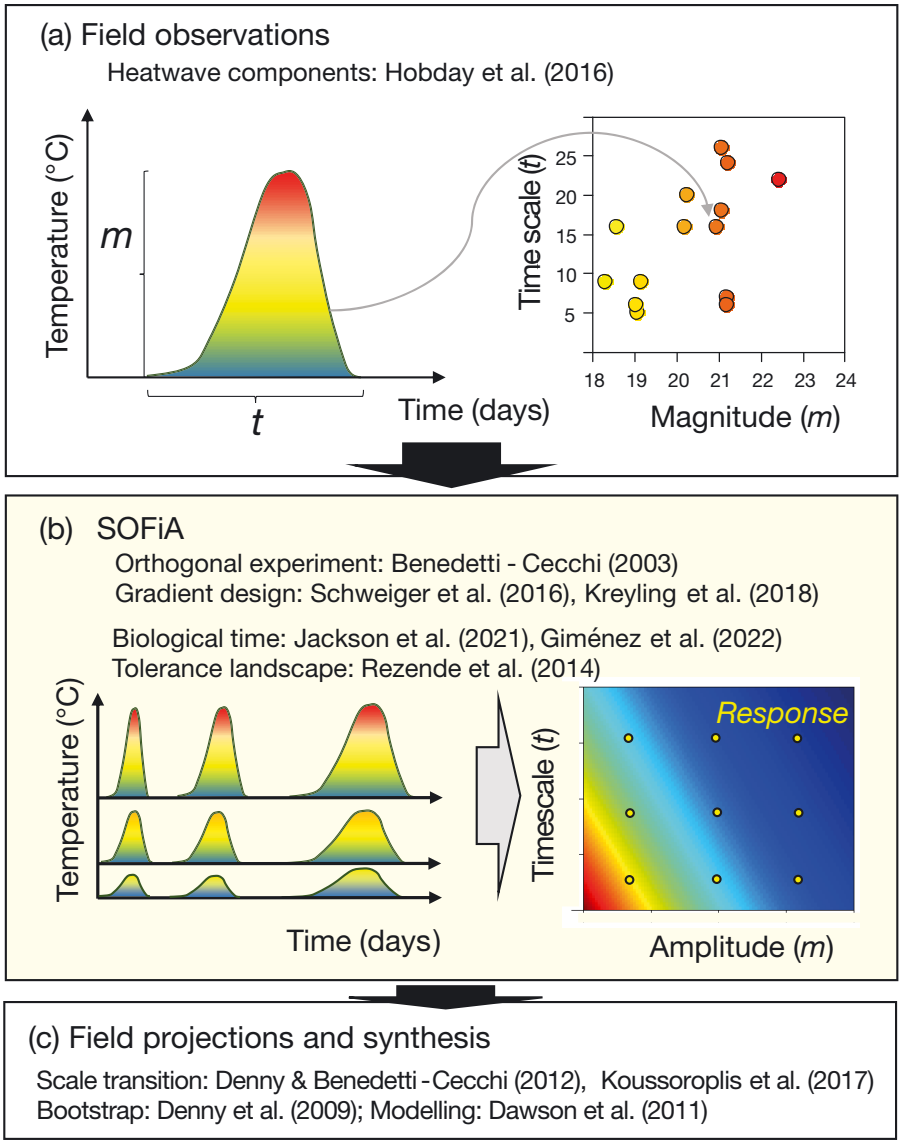

Fig. 2. SOFiA in the wider context of scaling experiments to predictions under field conditions. (a) Thermal fluctuations (e.g. heatwaves) vary considerably in amplitude (m) and time scale (t). (b) In SOFiA, an orthogonal experiment is carried out simulating fluctuations of different combinations of m and t; a response (e.g. body size as a heat map, with values decreasing from red to blue) is quantified at fixed locations (some represented as yellow points). In addition, organismal traits are used as a metric to define coordinate frames in which the additional biological responses are quantified. (c) Experimental results are used together with field data for models, projections (i.e. scenario analysis) or predictions. The references refer to literature providing ideas concerning one or more steps

The main issue with surface response designs is the large number of experimental units needed to cover the predictor space defined by the fluctuation components. For example, consider an experiment with 2 components and a maximum of 90 replicate units; 10 replicate units per treatment combination would constrain the experiment to 9 locations (i.e. 3 × 3 combinations of component values) in the predictor space. A potential solution is to use sequential experiments covering different regions of the predictor space at each stage (Box & Wilson 1951); however, this may be problematic if replicates are likely to vary in time for some reason other than the experimental random variation. An alternative solution is to either optimise the number of replicates or to use un-replicated designs, a technique known as 'gradient analysis' (Kreyling et al. 2018). For instance, at 90 replicate units, one may define 90 locations (as a 9 × 10 grid), allocating one unit each. Modelling exercises show that designs with low or no replica-

tion but many locations outperform replicated designs with fewer locations in detecting non-linear responses (Schweiger et al. 2016, Kreyling et al. 2018).

2.2. Fluctuation components

We need an approach that accounts for historical effects found at different levels of organisation. For instance, at the organismal level, acclimation and carry-over stress effects are pervasive (Giménez 2006, 2020, Pechenik 2006, Marshall et al. 2016) and can drive recruitment in marine populations (Torres et al. 2016). Historical effects are also important at the community level, and their evaluation requires the consideration of time scales explicitly in the design (e.g. see Dal Bello et al. 2017).

In the approach proposed here (Fig. 2b), fluctuations are characterised by an explicit time variable in addition to a magnitude variable (if only 2 components are considered). The use of the time variable enables us to capture any historical effect in addition to rescaling responses in biological time (see Section 4.4; Giménez et al. 2022). The use of a time variable helps us to move away from estimations of tolerance based on keeping organisms at constant conditions or using ramp experiments that do not necessarily match the time scale of natural environmental fluctuations (Terblanche et al. 2011, Rezende & Santos 2012, Gunderson et al. 2016). The choice of the magnitude variable depends on the situation; the present study focuses on amplitude to account for cases in which historical responses are associated with threshold phenomena (e.g. acclimation being triggered after some temperature level is experienced). In the field, time scales and amplitudes of fluctuations can be estimated through direct observations or from statistical models such as Fourier analysis or polynomial fitting. In this setup, projections or predictions (see Section 4.4) would be based on a response function matching the time scale of field-observed fluctuations.

3. THE SPACE OF FLUCTUATIONS

3.1. Coordinate frames

The central concept of SOFiA is that environmental fluctuations are characterised by a set of components and represented as points in a space. This multidimensional space resembles the one defined in multivariate analyses such as principal component analysis (PCA; or any other extension), where the principal components constitute a coordinate frame (Legendre & Legendre 2012). The space of fluctuations also has similarities with the concept of space state disturbance representation (Turner et al. 1993, Fraterrigo & Rusak 2008) but mostly with the tolerance landscape (Rezende et al. 2014), defined by the intensity and duration of a thermal stress. This concept may be expanded to a higher number of environmental variables (i.e. not only temperature), with a concomitant increase in the number of dimensions.

The second important point is that the metrics used to characterise thermal fluctuation components (e.g. for a heatwave: intensity measured in °C and time in days) are not unique or absolute. Instead, each point in the space of fluctuations can be located by using different coordinate frames. Here, the 'extrinsic frame' is the one defined by the 'observer', e.g. in clock time and °C. Further, the 'intrinsic frame' is defined as representing how the biological system under study experiences the fluctuations according to its own traits. For that purpose, biological variables are classified into 3 types. Type 1: variables with units of magnitude (e.g. thermal tolerance range) or time (e.g. days to maturation) or that drive tolerance and biological time; they give rise to the intrinsic frame. Type 2: invariant responses; a biological response that occurs within the tolerance range, does not drive tolerance or biological time and does not have units of time or magnitude. Type 3: biological rates or sensitivities; i.e. those expressed as per unit of time or tolerance. The role of each variable is introduced below.

As an example, the present work focuses on a study of the effect of thermal fluctuations on the body size (the invariant response) of a marine organism (e.g. invertebrate, fish), growing eventually to maturation. For the sake of the example, it is assumed that body size (the invariant response) does not drive tolerance or biological time. Biological time is the time to maturation; tolerance may be defined in a wide sense, i.e. as the range of preferred temperatures (Gvoždík 2018) based on the aerobic scope (Pörtner 2002), or a range defined from survival or knock-down temperatures (Tang et al. 2000). The same concepts can be applied to other levels of organisation; for example, biological time can be quantified for populations (generation time), communities (time scale of change in richness; Ontiveros et al. 2021), and ecosystems (inverse of ratio of production/biomass). Tolerance can also be defined for populations (Gvoždík 2018) and communities (Vinebrooke et al. 2004).

In the extrinsic frame (Fig. 2), the amplitude (m) is measured in °C and the time scale (t) is measured in clock time; e.g. in days (see Section S1, Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m721p017_supp1.pdf for variables and constants). The biological time scale of a fluctuation (τ) is a unitless quantity, corresponding to the proportion of time from birth to a relevant life history event (e.g. from birth to maturation). The biologically scaled amplitude of the fluctuation (μ) is defined as a proportion of the thermal tolerance range of the organism, i.e. the capacity of the organism to withstand environmental fluctuations.

The next element of the space of fluctuations is the time at which the observations are made. In the idealised experiment (Fig. 3a), organisms (originated in the same population) are exposed to fluctuations of different amplitudes and time scales. All organisms are kept at the same initial temperature, exposed to the fluctuations and then returned to the initial temperature before a measurement of body size is taken. The time at which body size is measured is expressed in clock ($t^\star$) and biological scales ($\tau^\star$). The observation times considered here (there may be several) occur after the fluctuation is experienced (Fig. 3a), i.e. $t^\star > t$ and $\tau^\star > \tau$). Observations must be done as the fluctuation occurs (see Section 4.4), but organisms must experience the full fluctuation before one can causally relate the response to the fluctuation time scale. The time course of the invariant response will occupy the full space of fluctuations, defined by the 3 axes: amplitude, time scale, and observation time (Fig. 3b). Because we assume that temperature drives developmental rates, the time points of observation at a fixed clock time will not coincide with those at a fixed biological time (e.g. at maturation). Therefore, observations at fixed clock vs. biological times will lie on different types of surfaces slicing the 3D space defined by the fluctuation components and the observation time. The invariant response, observed at a fixed clock time, lies on flat 2D time slices (Fig. 3b) of the space of fluctuations. In contrast, the response observed at a fixed biological time (e.g. at maturation) will lie on a curved surface (Fig. 3c), with its shape driven by the effect of temperature on the developmental rate (see next paragraph). Consequently, the pattern shown by the biological response will differ between the coordinate frames (Fig. 3c,d).

The next step is to define mathematical functions relating the components of the extrinsic frame (m, t and $t^\star$) with those of the intrinsic one (μ, τ and $\tau^\star$). The functions linking the clock with the biological time scales are given as: $\tau(t,m) = t \times L$ and $\tau^\star(t^\star,m) = t^\star \times L$ where $L(t,m)$ is the developmental rate, i.e. the inverse of the clock time (D) required to reach a particular biological event (e.g. days to maturation). Importantly, $L(t,m)$ is a function of the environmental fluctuation, not of the observation time (in line with the above-defined assumptions) and will be the inverse of the pattern shown by developmental time (Fig. 4a).

The biological scaled amplitude of the fluctuation, $\mu(t,m)$, is defined from thermal tolerance as $\mu = mS$. The function μ (unitless) varies between 0 and any positive value and quantifies the magnitude of the environmental fluctuation relative to the organismal tolerance range. The function S is the inverse of the tolerance range (E; Fig. 4b), which represents how sensitive the biological system is to the magnitude of the fluctuation. The case $\mu = 1$ corresponds to a fluctuation that encompasses the full tolerance range, while $\mu \to 0$ corresponds to situations where the organism is extremely eurytopic with respect to m ($S \to 0$ when m is very small with respect to the tolerance range). E is defined relative to some threshold; for instance, the so-called 'knockout temperature' (M_{out}, i.e. the temperature at which the organism dies or cease any activity, or does not respond to stimuli). In synthesis, E is the mathematical expression of the capacity of the organism to tolerate a fluctuation.

3.2. Invariant responses

The invariant biological response (body size; Fig. 3b) is a type of response that does not drive tolerance and it is not a rate of change with respect to any of the coordinate frames. The invariant response exists within the limits stated by the biological time and tolerance; i.e. there is a 'region of existence' within the space of fluctuations. This response is represented by a continuous and differentiable function, and the invariance property results in:

$$R(t,t^\star,m) = r(\tau,\tau^\star,\mu) \quad (1)$$

The invariance property is the reason that rates are not considered at this stage. Rates are partial derivatives of the invariant response (see below) and their magnitude depends on the coordinate frame. The differentiability assumption enables us to represent the effect of the thermal fluctuation on the

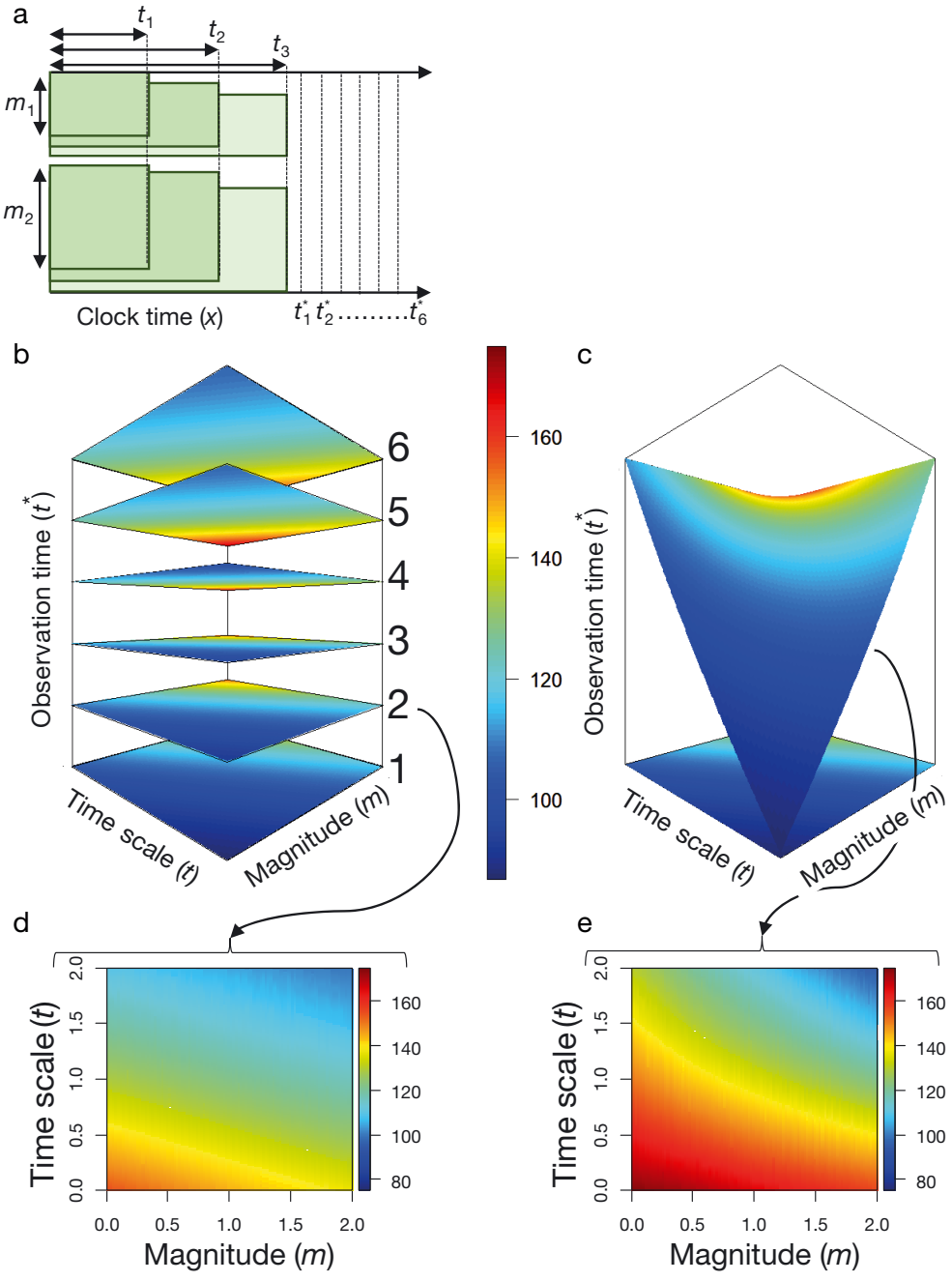

Fig. 3. Idealised time course of an experiment quantifying the effect of thermal fluctuations on the body size (colour scale, in arbitrary units) of an ectothermic organism at different times, including size at maturity, with the time of maturation driven by temperature. (a) Experimental design depicting a subset of the studied thermal fluctuations as rectangles of different magnitudes (m_1, m_2) and time scale (t_1, t_2, t_3); clock observation time are given as $t^*_1,\ldots,t^*_6$. (b) At fixed clock time, body size varied through time, occupying the volume defined by m, t and t^*. Body size, in response to m and t, lies on flat 2D slices (heat map) if observed at fixed clock times. (c) Body size at maturity, however, lies on a curved surface defined by the effect of temperature on biological time. Panels (d) and (e) illustrate how such an idealised experiment would show that the effect of thermal fluctuations on body size would depend on the time coordinate t^* or τ^*

response through partial derivatives with respect to the amplitude and period; the same idea applies to a general environmental fluctuation characterised by 2 or more quantitative descriptors. Hence, the effect of each variable of the invariant response is defined as a system of partial differential equations (PDEs; Giménez et al. 2022), which in matrix formulation gives:

$$\begin{bmatrix} \frac{dR}{dm} \\ \frac{dR}{dt} \\ \frac{dR}{dt^\star} \end{bmatrix} = \begin{bmatrix} \frac{d\mu}{dm} & \frac{d\tau}{dm} & \frac{d\tau^\star}{dm} \\ \frac{d\mu}{dt} & \frac{d\tau}{dt} & \mathbf{\frac{d\tau^\star}{dt}} \\ \mathbf{\frac{d\tau}{dt^\star}} & \mathbf{\frac{d\tau}{dt^\star}} & \frac{d\tau^\star}{dt^\star} \end{bmatrix} \times \begin{bmatrix} \frac{dr}{d\mu} \\ \frac{dr}{d\tau} \\ \frac{dr}{d\tau^\star} \end{bmatrix} \quad (2)$$

In a more compact notation, Eq. (2) may be written as $\boldsymbol{R} = \boldsymbol{M}\boldsymbol{r}$, where $\boldsymbol{R}$ and $\boldsymbol{r}$ are vectors of the derivatives of R and r, respectively; both $\boldsymbol{R}$ and $\boldsymbol{r}$ contain biological rates and sensitivities with respect to magnitudes and time scales. The matrix $\boldsymbol{M}$ transforms the rates of the intrinsic to the extrinsic frame; the inverse of $\boldsymbol{M}$ will do the reverse transformation. In Eq. (2), the third entry of the second row of $\boldsymbol{M}$ (in bold) is set to zero when the observation time varies independently of the time scale of the fluctuation (fixed clock observation time). In practice, $t^\star$ is constrained to be longer than the longest fluctuation time scale used in an experiment; however, within such limits, one can observe the response at any desired time. In addition, the first 2 entries of the last row of $\boldsymbol{M}$ (in bold) are set to zero because the observation time ($t^\star$, $\tau^\star$) does not affect the biological tolerance (i.e. μ) or the biological time scale of the fluctuation (i.e. τ). This follows from the fact that we ignore (for simplicity) the timing of the fluctuation as a component. In a more general case, such timing would be an additional component, giving an extra dimension to the space of fluctuations. Working with the response and the mapping functions is facilitated by 2 properties. (1) They should approximate continuous and differentiable functions so that the terms in $\boldsymbol{M}$ and the derivatives of R exist. Modelling of tolerance is sometimes carried out through conditional functions, but the alternative is to fit appropriate smooth functions to overcome the problem. (2) Mapping functions should be bijective (i.e. always increasing or decreasing), so as to provide a one-to-one mapping. Such functions ensure the existence of direct and inverse maps, from each point of the extrinsic to each point of the intrinsic frame. Not all functions of developmental time are like this; some show a minimum at an extreme high-temperature threshold followed by a maximum (Shi et al. 2017). Issues associated with (1) and (2) can be solved in practice by modelling different parts of the space of fluctuations as separate regions.

3.3. Scenarios of analysis

There are several scenarios for how the tolerance range and biological time drive the effect of the fluctuation on the invariant response. (1) The trivial scenario, in which neither E nor L are affected by the fluctuation traits. Both the extrinsic and intrinsic frames coincide, and the effect of the fluctuation on the body mass does not change with the coordinate frame. (2) A scenario in which E is not affected by the fluctuation traits. In such a case (discussed in Giménez et al. 2022), μ is proportional to m. (3) The scenario explored here, in which both E and L depend on some property of the fluctuation being experienced.

The nature of the intrinsic frame depends on how biological time and tolerance are shaped by the fluctuations. The present study considers 3 cases: in Cases 1 and 2, increased temperatures would result in a deleterious effect on performance (Niehaus et al. 2012). Case 1 is based on simple functions that help us to visualise and obtain a qualitative understanding of the differences between the extrinsic and intrinsic frames. Case 1 is related to Case 2, which introduces empirical functions and enables a realistic view of the chronic negative effects of fluctuations. Case 3 introduces adaptive plasticity, by which the fluctuation has positive effects on the tolerance range. In Cases 1 and 2, the response observed at a fixed clock time is simulated, whereas in Case 3, the time course of the response is simulated.

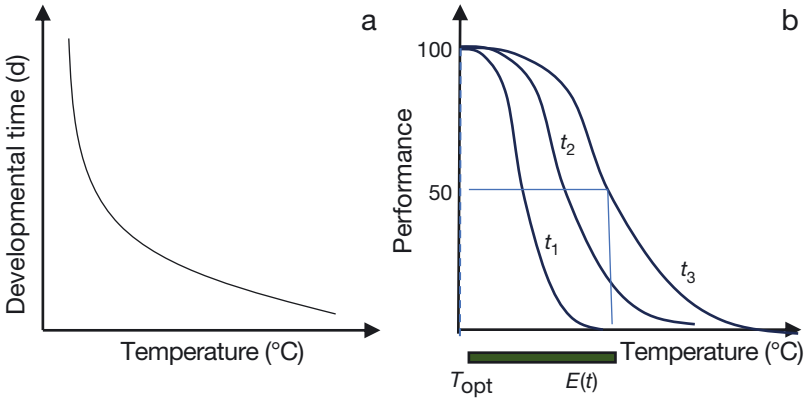

Fig. 4. (a) The curve of developmental time, showing a non-linear decrease with temperature; this curve is modelled subsequently in Eqs. (4) & (5) in Sections 4.1 and 4.2, respectively. Developmental time depends only on the amplitude of the thermal fluctuation $D = D(m)$ as in the case of phenology models based on degree days, but such an assumption does not restrict the analysis. (b) The tolerance range is defined for different fluctuation time scales (t_1, t_2, t_3), used to obtain the term S, included subsequently in Eqs. (3) & (6) in Sections 4.1 and 4.2, respectively

4. RESULTS

The central point in SOFiA is that the space of fluctuations is represented using different coordinate frames, related through non-linear functions. It is important to clarify the 2 different types of representations. First, one can represent a time slice defined either at a fixed clock time or at a fixed biological time (see Fig. 3b,c). Second, for each time slice, one can represent 2 projections based respectively on the extrinsic (*mt*-projection) or intrinsic coordinates (μτ-projection). For Cases 1–3, time slices at fixed clock time (fixed t^*) were focused on; this represents the simplest possible experiment and enables a better understanding of the different projections. The slice at a fixed biological time is explored in the worked example (Section 4.4). Given a (fixed) time slice, fluctuations are plotted in the upper half of a plane (Fig. 5a; details in Section S2 in Supplement 1), where $t > 0$ (fluctuations of negative time scale do not exist). In addition, none of the fluctuations will occur at $m = 0$ or $t = 0$ because such fluctuations do not exist either. For simplicity, it is assumed that $m > 0$ because experiments usually focus on either high or low temperature relative to a thermal optimum, for which m can be conveniently rescaled to be positive. Hence, the fluctuations of interest are plotted in the first quadrant (Fig. 5a) and the properties mentioned below do not change if m is negative.

4.1. Case 1: hyperbolic model

For tolerance, an inverse function $E = E(t) = 1/(S_0 + k_\mu t)$ was used, with $S(t) = (S_0 + k_\mu t)$. Here, S increases linearly with the time scale of the fluctuation, from a minimum (S_0) defined as $1/T_{max}$; the constant k_μ is a rate of increase. In such a case we obtain:

$$\mu = m(S_0 + k_\mu t) \quad (3)$$

In addition, it is assumed that developmental time follows an inverse function of temperature, such that:

$$\tau = t(D_{min} + k_\tau/m)^{-1} \quad (4)$$

where D_{min} is the asymptotic minimum developmental time achieved as $m \to \infty$, in the absence of developmental impairments.

The values of the intrinsic frame define a non-linear and non-orthogonal coordinate frame (Fig. 5b). Eqs. (3) & (4) define hyperbolic curves, as lines of equal τ (or μ) in a similar way as the straight lines in Fig. 5a define lines of constant m or t. Consecutive lines define areas of different size, with the shape of such areas depending on the constants (S_0, D_{min}, k_μ, k_τ) driving the tolerance and developmental time. Such lines do not meet at straight angles, reflecting the fact that μ and τ are not mutually independent variables.

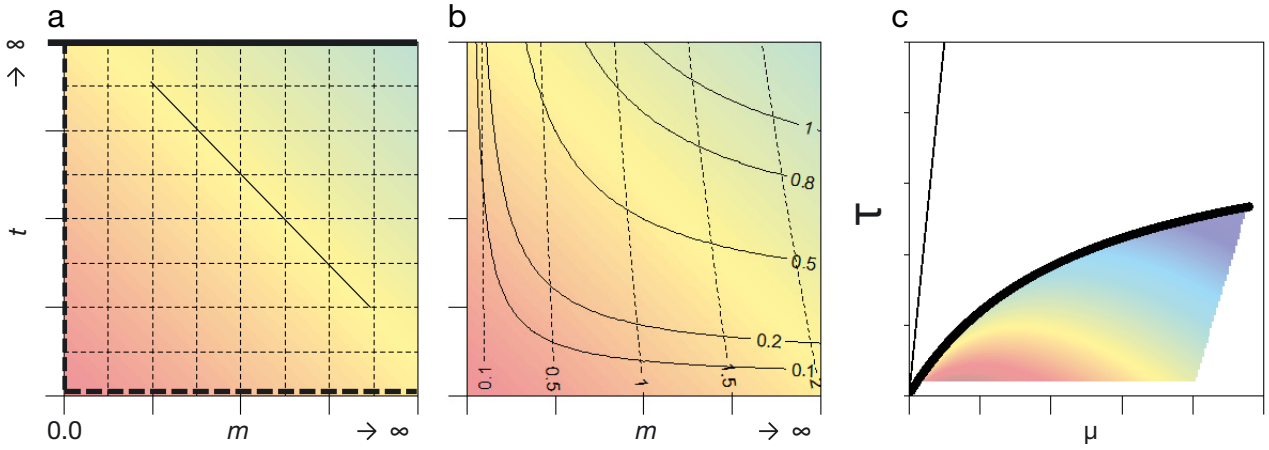

Fig. 5. A time slice of the space of fluctuations at a fixed clock time, showing a biological response $R = 100 - t - m$ as a heat map. (a) *mt*-projection with *mt*-isolines given by straight lines (i.e. as a Cartesian frame). In the heatmap of R, isolines (lines indicating equal R-values) are given by diagonals (note colour gradient) and one such diagonal is shown as a continuous line. The horizontal top line represents the line at infinity corresponding to constant conditions. Dashed lines at $m = 0$ and $t = 0$ are open boundaries. (b) *mt*-projection with μτ-isolines given by curves (here taken from Case 1), with all parameters of Eqs. (3) & (4) set to = 1, except $k_\mu = 0.1$. (c) μτ-projection. The space occupied by the fluctuations is constrained to the coloured area by the maximum values of m and t; these represent the maxima used in a realistic experiment. Thick black curve: the upper limit set by the maximum value of t; straight line: the theoretical maximum. Isolines of equal body size (diagonals in a and b) form petal-like curves in (c) and the parabolas of (b) would give straight lines in (c)

An alternative view of the response, highlighting the organismal perspective, is given by the 'μτ-projection' (Fig. 5c). This is analogous to the projection obtained from a PCA, where communities are represented as points in a space. Before the PCA is carried out, the original projection (an analogue to the *mt*-projection here) would have species abundances as axes. The difference is that the PCA axes are linear and orthogonal, while μτ axes are curvilinear and non-orthogonal. Consequently, in the μτ-projection, the fluctuations are constrained to a triangular region characterised by open boundaries (coloured area in Fig. 5c) and the region is set by logistical and theoretical limits (see Section S2).

Provided with the projections defined above, and focusing on the perspective of the organism, the following points are highlighted:

(1) Space of existence. The region where $\mu \leq 1$ and $\tau \leq 1$ defines the 'space of existence', i.e. where the response, R, exists. This is because $\mu > 1$ implies that the temperature is higher than the tolerance range (hence the organism collapses). In addition, $\tau > 1$ implies that the time scale of the fluctuation is longer than the time to maturation; therefore, one cannot establish a causal relationship between biological time and the fluctuation time scale. In other examples, the space of existence will be set at $\tau \neq 1$ (see Section 5).

(2) Extreme events and the biological definition of a heatwave. Extreme events (i.e. a fluctuation compromising organismal existence) are represented by the set of fluctuations defined by the curve $\mu = 1$. Notice that such a curve defines fluctuations that differ in amplitude and clock time scale. If extreme events are used as a biological definition of heatwave, then such a definition would differ from that based on climatology. For instance, marine heatwaves are defined as those thermal fluctuations in which the temperature exceeds a fixed threshold (the 90th percentile of a temperature distribution) for 5 or more days (Hobday et al. 2016). IN contrast, the definition arising from the μ-curves does not use fixed temperature and time scales.

(3) From the standpoint of the organisms, differences among fluctuations are defined by the values of μ and τ (not m and t). From the extrinsic perspective, straight lines (i.e. the Euclidean distance) should define the difference (= shortest distance) between any 2 fluctuations (Fig. 5a; also recall the analogy to PCA for ecological communities). However, from the intrinsic perspective, the shortest distance between any 2 fluctuations is given by the hyperbolic curves (Fig. 5b). Hence, whether 2 fluctuations are experienced by the organism as very different or rather similar depends on the distance along the hyperbolic curves. In this case, the projection in the μτ-plane (Fig. 5c) might give a more intuitive view of the differences among fluctuations from the organismal perspective.

(4) The invariant response (body size at maturation) is distorted as we compare the different projections (Fig. 6). The distortion reflects important biological effects of temperature on both tolerance and biological time. In the simulation (see Section S3 in Supplement 1 for details), the invariant response is more sensitive to m than to t (equation in Fig. 6) but it becomes more sensitive to τ than to μ (compare the change in colour gradient in Fig. 6a vs. Fig. 6b). The distortion reflects the fact that the organism will experience the response as being different from what is shown by the extrinsic frame.

Next, Case 2 uses realistic functions and highlights (by comparison to Case 1) properties that are robust to changes in the mapping functions.

4.2. Case 2: combining metabolic theory and thermal tolerance

Case 2 considers empirically obtained functions for developmental time and tolerance and uses *mt*-projection to focus on the region of existence and on

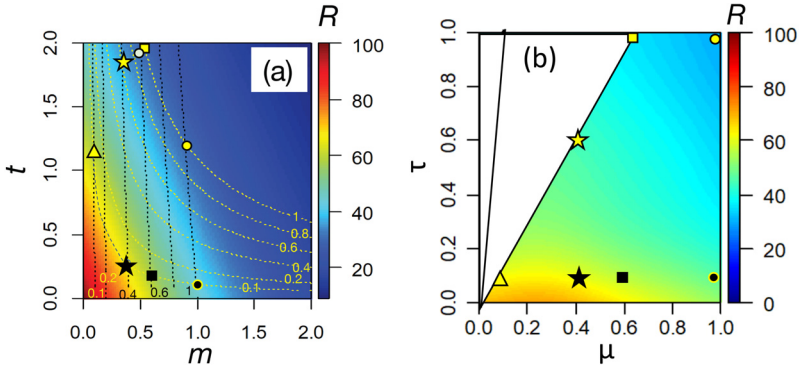

Fig. 6. A time slice of the space of fluctuations at fixed clock time (a) *mt*-projection with intrinsic coordinate frame included; (b) μτ-projection. Different symbols in (a) represent fluctuations which are shown in (b) to highlight the deformation produced by the intrinsic frame. The diagrams were constructed within the range (0, 2) for both t and m. The mapping functions are as follows: Eq. (3): $S_0 = 1$, $k_\mu = 0.1$; Eq. (4): $D_{min} = 1$, $k_\tau = 1$. The response was modelled as $R = 100 \times \exp(-0.4m - 0.8t)$

the definition of extreme events. Developmental time is defined in the metabolic theory of ecology of Brown et al. (2004) such that:

$$\tau = tL_{max} \times e^{\frac{-A}{(m+273)}} \quad (5)$$

where m is the temperature (in °C), L_{max} is the inverse of the asymptotic minimum of developmental time and A is the ratio of activation energy (0.64 eV, 1.025×10^{-19} J) and the Boltzmann constant (8.617×10^{-5} eV K^{-1}, 1.381×10^{-23} J K^{-1}).

The effect of the fluctuation is modelled following work on thermal death times (Bigelow 1921, Urban 1994, Tang et al. 2000, Rezende et al. 2014, Jørgensen et al. 2019). Those studies show that responses to temperature can be modelled with 2 separate functions: (1) a thermal range characterised by moderately high (or low) temperatures, where survival is independent of the exposure time. Responses in this range are equivalent to those covered in Giménez et al. (2022), where μ is proportional to m because E would not vary with time. (2) Beyond a thermal threshold, E decreases linearly with the logarithm of exposure time. I focus on this range,, assuming that the tolerance range is proportional to the logarithm of the time scale of the fluctuation. Here, $E(t)$ depends on the knockout temperature (i.e. M_{out}) according to the equation $M_{out} = M_{crit} - z\varepsilon_1 \log(t\varepsilon_2)$. Here, M_{crit} is the knockout temperature corresponding to a unit of clock time (t = 1), z is the sensitivity of M_{out} to the change in log(t). In addition, ε_1 and ε_2 are proportionality constants (= 1) and are no longer considered. By setting $E_{max} = M_{crit} - M_0$ (maximum tolerance range with respect to the optimal temperature, M_0), we obtain: $E(t) = E_{max} - z\log(t)$. In such a case, the biological magnitude in the intrinsic frame (μ) is given by the equation:

$$\mu = \frac{m}{[E_{max} - z \times \log(t)]} \quad (6)$$

As in Case 1, the lines at μ = 0 and τ = 0 are open boundaries, and the lines of constant μ or τ are curves, representing a non-orthogonal reference frame that will also deform any invariant response (further similarities discussed in Section S4 in Supplement 1). In the *mt*-projection, values of μ (heat maps in Fig. 7) capture the general pattern observed by studying thermal death times, i.e. low-amplitude but long-period fluctuations can be as bad as high-amplitude short-period ones.

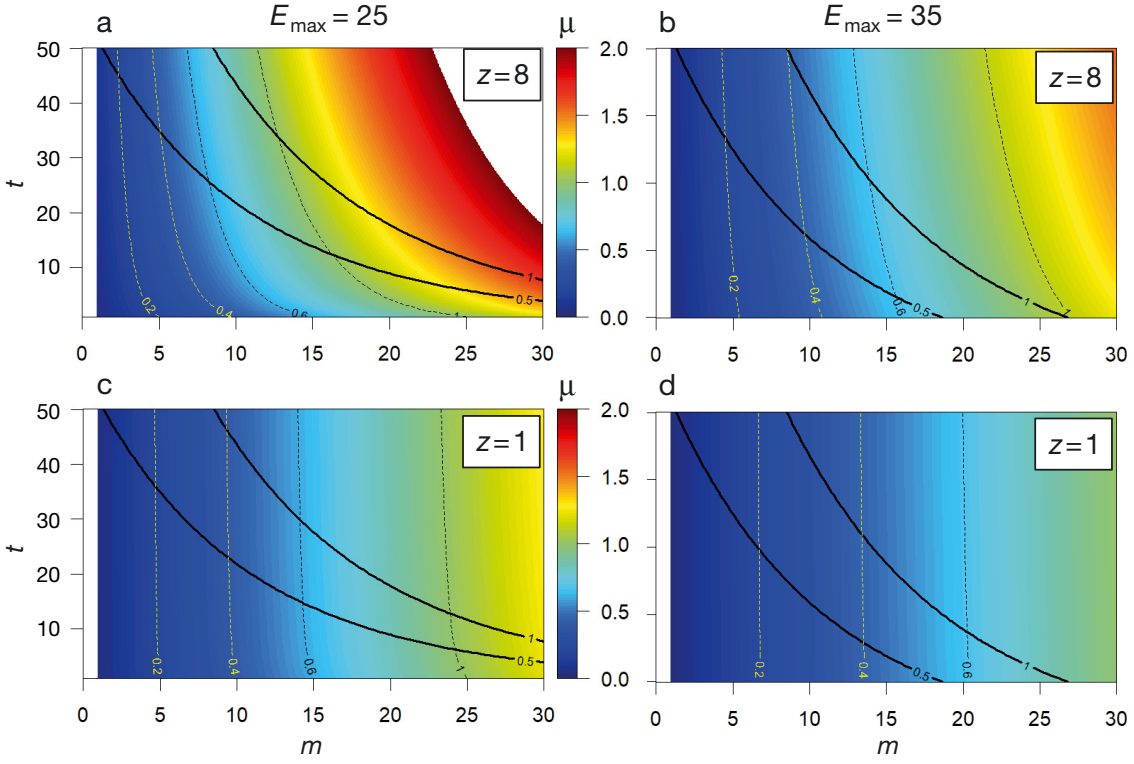

Fig. 7. Case 2: a time slice of the space of fluctuations at a fixed clock time showing a heatmap of μ based on Eq. (6). Each panel has different values of z and E_{max} (i.e. tolerance range at t = 1). Dashed lines are selected lines of constant μ: note that at small z, μ becomes proportional to m and less dependent on t. Continuous lines are lines of constant τ (Eq. 6; $L_{max} = e^{22.47}$)

Case 2, based on empirical models, again gives a definition of an extreme event as in Case 1, where the critical temperature defining the heatwave (here represented as m) depends on the clock time scale of the thermal fluctuation (Fig. 7); here, the position of the curve $\mu = 1$ depends on $\log(t)$. In addition, the set of extreme fluctuations and the region of existence depends on the thermal sensitivity (z) and the maximum tolerance range (E_{max}). At high z and narrow E_{max} (Fig. 7a), the region of existence is constrained to fluctuations that are shorter than the time to maturation ($\tau = 1$). In the simulation, there is only a narrow region ($t > 30$ in Fig. 7a) where the curve of the extreme fluctuations ($\mu = 1$) is located to the right of the curve of $\tau = 1$. This indicates that extreme fluctuations occur at time scales longer than the time to maturation. At other combinations (Fig. 7b–d), such a region expands; for instance, for $z = 1$ and $E_{max} = 35$, most of the extreme fluctuations occur at time scales that are longer than time to maturation (Fig. 7d).

It is important to note that the interpretation of the isolines $\mu = 1$ and $\tau = 1$ depends on the specific case. For example, it may not be possible to quantify tolerance beyond maturation, i.e. in the region located to the right where $\tau > 1$ (the maximum time scale covered in the experiment). Likewise, in the region where $\mu > 1$, developmental time cannot be quantified. However, tolerance may be quantified in the region where $\tau > 1$ in the case of e.g. a multigenerational study where the biological time is defined as generation time. In an example of organisms growing to metamorphosis (instead of maturation), scenarios in which the curve $\mu = 1$ is located to the right of $\tau = 1$ would indicate that reaching a critical life history stage (e.g. metamorphosis) has the potential to 'rescue' the organism (or population) from the consequences of an extreme fluctuation. For species experiencing metamorphosis and habitat shifts, thermal conditions before the shift may not be the same as in the post-shift habitat. Alternatively, organisms may experience shifts in their capacity to tolerate increased temperatures, for instance in association with metamorphosis: larval stages are usually more sensitive than juveniles and adults (Pandori & Sorte 2019). In both cases, reaching metamorphosis would be analogous to reaching a thermal refuge. In semelparous species, reaching maturation and reproduction ($\tau = 1$) is central, but post-reproductive life ($\tau > 1$) is of no relevance for fitness. In any case, SOFiA captures important aspects of ontogeny, physiology and phenology as drivers of responses to extreme events.

4.3. Case 3: role of adaptive plasticity

In the above cases, tolerance depended only on the time scale of the fluctuation. However, the presence of adaptive plasticity should (within limits; DeWitt et al. 1998) either shift or expand the tolerance range (Angilletta 2009 chapter 5, Seebacher et al. 2014, Salachan & Sørensen 2022) in response to the (thermal) fluctuation. We can visualise the rescue effect of adaptive plasticity as an expansion of the space of existence in the mt-representation (see below).

Plasticity involves 3 main steps (Windig et al. 2004): (1) a cue is converted to a signal (e.g. hormones; Duffy et al. 2002) that (2) triggers a change in the phenotype, which results in (3) a change in its performance (= tolerance). Those steps lead to a latency period (Laubach et al. 2022) between the moment when an environmental cue is detected and when the phenotype is functional. The latency period varies according to the type of plasticity, from short (hardening; Hoffmann et al. 2003) through developmental (Salachan & Sørensen 2017) to transgenerational plasticity (Donelson et al. 2018). The relationship between the latency period and the time scale of the fluctuation may range between 2 extremes. At one extreme, the fluctuation may be perceived as a short-term pulse with respect to such a period (Manenti et al. 2018), while at the opposite extreme, the fluctuation is perceived as a long period wave. In the first case, the tolerance range depends on whether the organisms (or the parents) experienced a previous fluctuation. In such a case, we may define the acclimation state of an organism as $E_i(t)$, which will shift from $E_1(t)$ to $E_2(t)$ after a fluctuation is experienced. One may model such a change of state as a change in the parameters defining the equations of Case 2 (see Section 4.2).

The present study focuses on the case (Fig. 8) in which the latency period can be much shorter than t so that (1) the acclimation state changes as the fluctuation is experienced and (2) the fluctuation can be sufficiently long to alter developmental time. An example is the acclimation to seasonal fluctuations in temperature in which organisms acclimate to summer (or winter) conditions well in advance of the time of maximum (or minimum) temperatures. Those steps are modelled through functional responses, with the overall result that changes in the cue (temperature) are mapped into changes in the thermal tolerance and μ (Fig. 8). This simulation differs from Cases 1 and 2 in that here the time course of the response is modelled (details in Section S5 in Supplement 1). It was not the intention to develop a mechanistic model (see e.g.

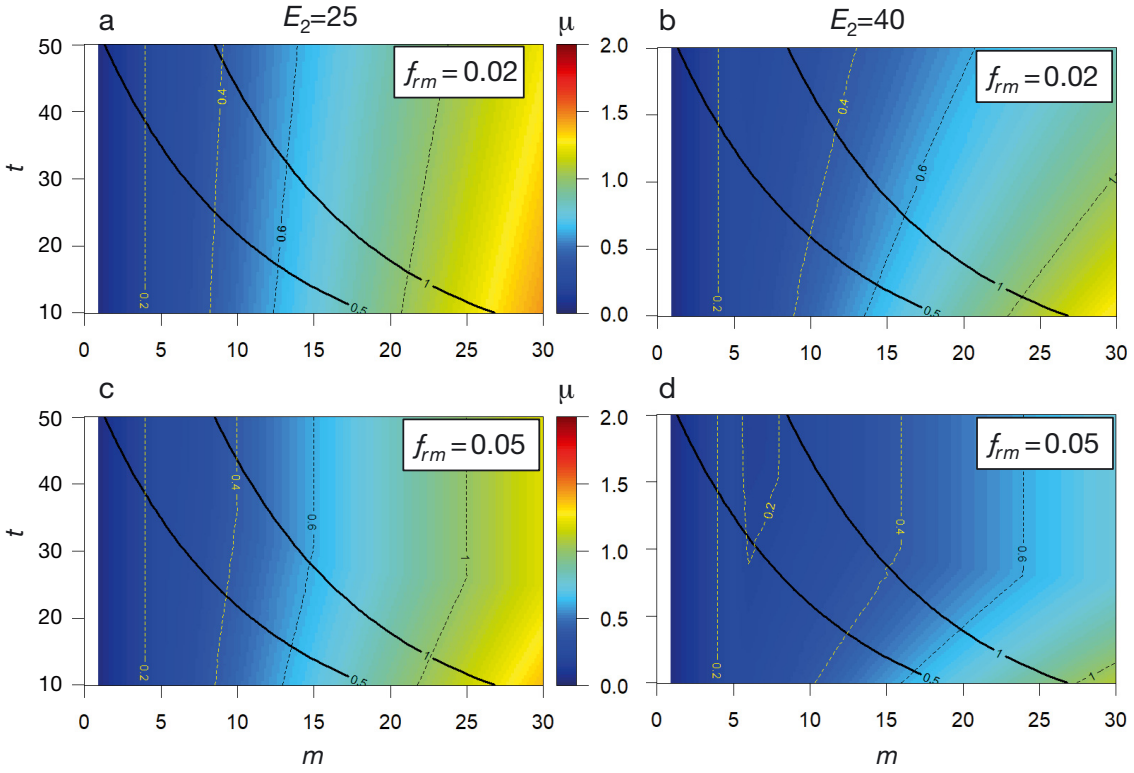

Fig. 8. Case 3, adaptive plasticity: a time slice of the space of fluctuations at a fixed clock time showing a heatmap of μ. Different panels (a–d) show μ for different values of maximum tolerance range (E_2 = 25 and E_2 = 40) expanded from a value of E_2 = 20 before the fluctuation is experienced. Inset values correspond to the maximum rate of phenotypic change (f_{rm}) as driven by temperature (equations in Section S5 in Supplement 1). In all panels, the signal activation threshold was at 5°C; this is best noted at E_2 = 40 and r_{max} = 0.05. Continuous lines: constant τ-values; dashed lines: constant μ-values

Hazel et al. 1990, Buoro et al. 2012) and it must be emphasised that the model is intended as an illustration of how plasticity can be incorporated into SOFiA.

The rescue effect of adaptive plasticity is shown as the expansion of the region of existence: the curve μ = 1 is shifted to the right (compared to Cases 1 and 2). Hence, the rescue effect is manifested in the set of fluctuations defining extreme events. Compared to the previous cases, extreme events occur at high values of m. The region where the plastic response operates depends on 3 main steps.

(1) The threshold response to the cue: below some thermal threshold (fixed to 5°C in Fig. 8 and 10°C in Fig. S4 in Section S5), the plastic response is not triggered (m < 5°C in Fig. 8). The tolerance range is still wide (giving low μ values). In the model, the threshold response is driven by the thermal threshold y_u of the first functional response:

$$F_{c\to s} = \frac{1}{1+e^{k_s[y_u - y(x)]}} \quad (7)$$

where $F_{C\to S}$ is the function converting a cue to a signal, $y(x)$ is the temperature fluctuating through clock time (x) and k_s is a rate constant indicating how sharp the triggering of the response is.

(2) The rate of phenotypic change in response to temperature f_r:

$$f_r = \frac{f_{rm} \times y}{k_r + y} \quad (8)$$

where f_{rm} is the maximum rate of phenotypic change and k_r is the half-saturation constant in the model; the inverse of f_{rm} is a time scale, defined here as the minimum latency period.

This rate is the component of the second functional response:

$$F_{S\to P} = f_{sp1} + \sum_x f_{r(x)} \quad (9)$$

$F_{S\to P}$ maps the signal to the phenotypic state (as a continuous variable) from an initial state, f_{sp1} (before the signal activates the response), up to an upper threshold = f_{sp2}, remaining constant thereafter. Because Eq. (9) has an asymptotic maximum (f_{rm}), the rate of phenotypic change is constrained; as a consequence, if the time scale of the fluctuation is sufficiently short, there is no sufficient time for the plastic response to reach its maximum value. Hence, plasticity operates on the μ values at intermediate values or m and t (at moderately high m).

(3) The maximum thermal tolerance range, defined in the third functional response of the model $F_{C\to S}$, which maps the phenotype to the thermal tolerance. This function is linear between the lower (= E_1) and the upper tolerance range (= E_2) and defines the region of existence in Fig. 8.

4.4. Worked example

The worked example (Fig. 9; details in Section S6 in Supplement 1 and data files in Supplement 2 at www.int-res.com/articles/suppl/m721p017_supp2.xlsx) represents an experiment aimed at (1) quantifying the effect of the magnitude and time scale of thermal fluctuations on the body size of a marine ectotherm and (2) estimating the average body mass, given a set of fluctuations of varying magnitude and time scale. The example represents experiments taking place over several weeks to a few months, which corresponds to those carried out with short-lived organisms (e.g. copepods) or a specific life phase of a long-lived species (e.g. larvae). Biological time is referenced up to maturation (copepods) or metamorphosis (fish or invertebrate larvae). In both cases, temperature has a strong effect on developmental time (copepods, Guerrero et al. 1994, McLaren 1995; marine larvae, O'Connor et al. 2007); hence, the functions mapping the time coordinates are important. For example, within species, increased temperature can reduce larval developmental time by 50% over the tolerance range, which can span 10–15°C (but varies among species; O'Connor et al. 2007). Increases of only 3°C can result in important reductions in developmental time towards the lower sector of the thermal tolerance range. For example, in one of the best-studied crustaceans, the shore crab *Carcinus maenas*, an increase in temperature of 3°C reduces the larval developmental time (to megalopa or first crab stage) by 25–35% within the range 12–18°C, corresponding to summer temperatures in the distribution range (Dawirs 1985, DeRivera et al. 2007, Šargač et al. 2022). The functions mapping time coordinates become more important at that sector, especially under long fluctuation time scales. At the upper sector of the thermal tolerance range, biological time is affected little by temperature; however, at that sector, the functions mapping from the extrinsic to the intrinsic magnitude coordinates should become important if tolerance depends on the time scale of the fluctuation.

The experiment follows a gradient design (Kreyling et al. 2018) with 10 levels of thermal magnitude

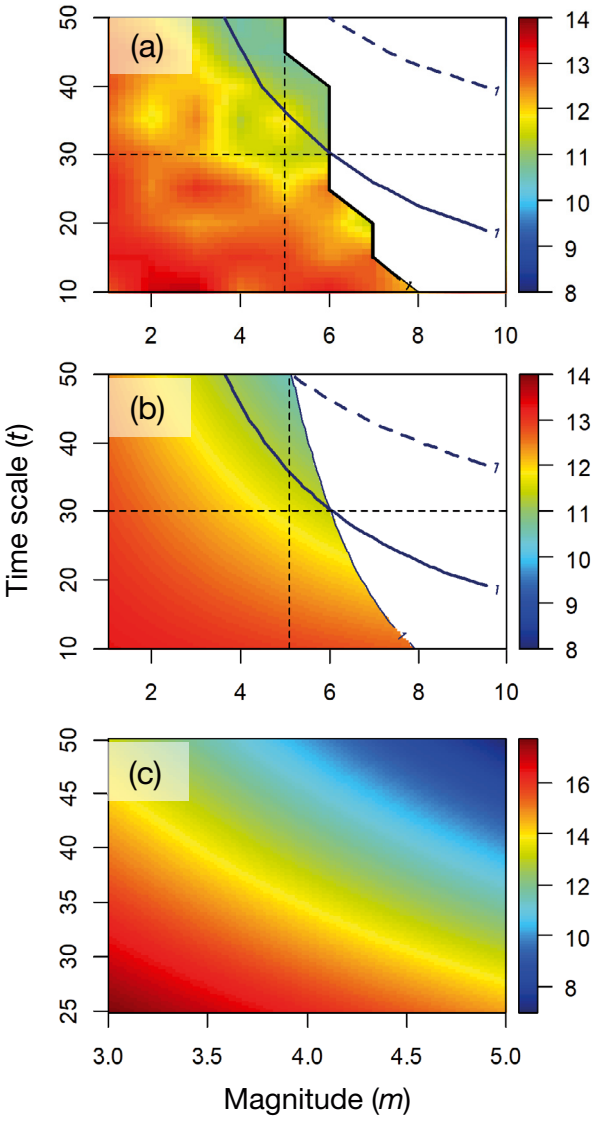

Fig. 9. Worked example. Simulation of an experiment quantifying the role of magnitude and time scale of thermal fluctuations on body size (colour heatmap) of a marine organism at maturation. (a) *mt*-projection of the observed response at a fixed clock time ($t^\star$ = 70 d). (b) Fitted curves and body size at the same fixed clock time as in (a). (c) *mt*-projection of the fitted response at maturation. The projections in (a) and (b) correspond to a flat time slice (see Fig. 3); the $\mu = 1$ curve is the black line delimiting the white area (i.e. no data at $\mu > 1$). The curve of the time at maturation, $\tau^\star = 1$, is given as a continuous blue line; dashed blue line corresponds to the curve of $\tau = 1$ (fluctuation with time scales of the maturation time). The curves of $\tau^\star$ and τ differ because they are scaled to different time variables. Vertical dashed line: the region (to the left) where maturation is reached irrespective of the time scale of the fluctuation; horizonal dashed line: an upper region where maturation can be reached. The heatmap in (c) lies on a curved surface (see Fig. 3) and it is restricted to the region of the space of fluctuations enabling maturation (note axis ranges). The data (csv file) and procedures are given in Section S6 (Supplement 1) and Supplement 2

crossed with 9 levels of time scales, giving 90 locations (i.e. combinations of time scales and magnitudes) in the space of fluctuations. Organisms are observed every day in order to record the time at maturation and the time at which they reach the thermal limit (i.e. they die or exhibit a predefined behavioural response). In the first step, non-linear regression models are used to obtain the equations giving τ, μ, size after 70 d of the experiment ($R_1[m, t, t^\star = 70\ \mathrm{d}]$) and size at maturation ($R_2[m, t, \tau^\star = 1]$). For the second objective, the functions R_1 and R_2 are used to estimate the average response through scale transition theory, model simulations and the so-called mean field approach.

The constraint on the number of times size can be observed reproduces a realistic experiment in which animals die beyond the region of existence and measurements of body size are too invasive to be performed more than twice, or where there are logistical constraints. With some caveats (see next paragraph), the example may also be taken as a case study of a species monoculture (e.g. macroalgal or mussel bed) or natural community that is recovering after a disturbance event, in which the biological variables are generation time (or the inverse of species replacement rate), tolerance (or species richness) and biomass (or some ecosystem service).

In the worked example, the curves $\mu = 1$ and $\tau = 1$ cross each other as expected if some of the fluctuations enable maturation but others kill organisms before reaching maturity. In other situations, such curves may not cross but the experiment will still provide valuable information. If all animals reach maturity, the experiment will quantify the dependence on body size on the time coordinate frame. If, by contrast, thermal thresholds are reached before maturation, the experiment would provide information about the region of existence and identify the set of fluctuations defined as extreme (i.e. the set defined by the curve $\mu = 1$).

The importance of the mapping function is given by the following points. First, the function $\tau^\star(m, t, t^\star)$, which maps coordinates of observation time, shows that responses differ considerably depending on whether we quantify size at maturation or at a given clock time. The difference is shown in Fig. 9 (contrast Fig. 9a,b vs. Fig. 9c) and in the estimated body size given an average heatwave (Table 1; compare R_1 vs. R_2). Second, the function $\mu(m, t)$ quantifies the effect of the time scale of the fluctuation on thermal tolerance; it predicts which heatwaves would result in system collapse. This is illustrated in Fig. 9b as the white area, which corresponds to heatwaves with combinations of magnitudes and time scales (m and t coordinates) giving $\mu(m, t) > 1$. Third, the combination of the abovementioned functions predicts the set of heatwaves that still enable animals to be 'rescued' by achieving maturity (or metamorphosis). This is illustrated in Fig. 9b as the portion of the curve $\tau^\star = 1$ lying at the left of the curve $\mu = 1$ (i.e. not in the white area). Fourth, the combination of $\mu(m, t)$ and $\tau(m, t)$ predicts the set of fluctuations that are not tolerated and are characterised by a time scale equal to the time to maturation (or to metamorphosis). This is illustrated in Fig. 9b with the curve $\tau = 1$ (dashed line) lying at the right of the curve $\mu = 1$, if $m > 5$; the portion lying to the left of the curve $\mu = 1$ is predicted to occur if larvae experience fluctuations of time scales larger than 50 d.

In interpreting R_1 and R_2 (Fig. 9b,c), one must recall that such functions are on different surfaces that cut the volume representing the time course of the invariant response (Fig. 3). The difference between R_1 and R_2 (Fig. 9b,c) is shown by modelling the average response (Table 1) to a set of fluctuations (Fig. 9c), but in both R_1 and R_2, the mean field approach underestimates the average response compared to simulations from the model or applying scale transition theory.

5. DISCUSSION

This work presents a geometric approach (SOFiA) to understanding biological responses to temperature (or other environmental fluctuations) from the perspective of organisms. This approach expresses the organismal perspective as a coordinate frame within a space defined by fluctuation components and the times at which observations are made in an experiment. Using temperature as an example, it is shown how this approach integrates our current knowledge about the effects of environmental variables on organisms. We know that temperature has a strong non-linear effect on biological time (McLaren 1995, Gillooly et al. 2002), that thermal tolerance decreases non-linearly with exposure time (Rezende et al. 2014)

Table 1. Estimated body size (in arbitrary units) at $t^\star = 70$ d (R_1) and at maturation (R_2) based on mean field approach, scale transition theory and model simulation

	R_1	R_2
Mean field	11.95	14.12
Scale transition	11.92	14.03
Simulation	11.92	14.03

and that adaptive plasticity has a characteristic time course (Windig et al. 2004). The organismal perspective is obtained from the relationship between different types of biological traits: (1) traits driving tolerance and biological time provide the metric for the biological scaled magnitude and time of a fluctuation; (2) there are traits, called invariant responses, that respond to tolerance and biological time; and (3) traits defined by rates are identified as those with a magnitude that depends on the reference frame. In addition, the geometric approach presented here highlights the importance of considering the frame used to scale the time at which observations are made because of its consequences in the observed invariant response. The result is the capacity to quantify biological responses in different frames, which should lead to a better mechanistic understanding; in addition, the approach presented here can provide predictions for field conditions (through e.g. scale transition theory, as shown in Section 4.4).

A main feature of SOFiA is the mathematical formalism, represented by a set of functions and PDEs. One may argue that this is merely a formalizing exercise, only providing more precision. However, the mathematical formalism is central to identifing counter-intuitive results that arise from interactive effects and non-linearities. A similar approach has helped to identify the conditions where interactive effects, occurring at a level of organisation (e.g. individuals), are not mapped into a higher level of organisation (population; DeLaender 2018). Likewise, the mathematics of scale transition theory (Denny & Benedetti-Cecchi 2012) are needed to determine when (and to what extent) the average of the biological response does not match the response to the average temperature. In all those cases, quantitative predictions are not those expected from intuition. The approach presented here deals with non-linearities and interactive responses to the predictors (as above), and non-linear transformations between different frames. For example, the solutions of PDEs can help us to identify scenarios when the type of multiple driver response depends on the metrics of time (see Section 4.4, Fig. 9 and Giménez et al. 2022). Given only 2 components of a single fluctuation (magnitude and time scale), we can still rely on 2D graphical representations for a better understanding of a response that depends on the coordinate frames, as illustrated in Fig. 3 (i.e. the response on different surfaces). However, in cases of 2 or more fluctuations (e.g. temperature plus a second environmental variable), the responses will lie on higher dimensional surfaces and intuition will be of limited help. It seems that, as the field progresses, the stronger mathematical emphasis will constitute an important guide to navigate through the complexity of high dimensional phenomena, interactive effects and non-linearities. Hence, the mathematical analysis used here may be considered an additional step in the processes summarised in Fig. 2, helping with the design and interpretation of experiments as well as the application scale transition.

SOFiA incorporates the biological perspective, defined by the time scale and the capacity of organisms and other biological systems to cope with environmental fluctuations. The first important concept is the 'region of existence', defined from fixed values of μ and τ (both set to 1 in the example). This is an important point in light of discussions concerning the definition of heatwaves (Bailey & van de Pol 2016, Hobday et al. 2016, Jacox 2019). From a biological standpoint, heatwaves would be defined as the set of extreme fluctuations (characterised by $\mu = 1$) that depend on the time scale of the fluctuation. Many studies have shown that tolerance to a given stressor scales with the inverse of the logarithm of the time of exposure (revision in Rezende et al. 2014). Such a biological definition would incorporate the rescue effect produced by adaptive plasticity. Simulations in Case 3 highlight the importance of time delays in the expression of the plastic response in determining the set of extreme fluctuations.

The starting point in SOFiA was to consider fluctuations as a collection of components (as in Hobday et al. 2016) and define fluctuations as objects existing in a hypervolume in the same way that ecologists define elements in the ecological niche (Blonder 2018) or characterise communities (e.g. Legendre & Legendre 2012). At the organismal level, the space of fluctuations has connections with the concept of tolerance landscape (Rezende et al. 2014) where the response is tolerance, existing within a space defined by the magnitude and time scale of exposure to a particular stressor. At the species level, there are connections with the Hutchinson view of the niche (i.e. where resources or environmental variables define the axes), but adding time variables and meeting the needs of incorporating phenology into the concept of the niche (see Ponti & Sannolo 2022). In addition, for both cases, the main contribution of SOFiA is the quantification of the perspective of organisms through additional reference frames.

Different perspectives, including that of the observer, are related through mapping functions (from t to τ and m to μ). We can also consider a case with 2 different frames representing 2 different species; in

such a case, we can remove the reference frame of the human observer from the equations (see Section S7 in Supplement 1) and project the response of the first species from the perspective of second one. The framework can also be used to visualise biological responses underpinned by different mechanisms (or based on empirical fits) of how tolerance and biological time respond to a given fluctuation. For example, the comparison among Cases 1–3 helps us to identify properties that are contingent on the presence of plasticity or the adoption of a specific type of trade-off between critical temperature and tolerance period. In addition to the metabolic theory of ecology, the response of developmental time has been predicted from theory or other equations (Ahlgren 1987, Guerrero et al. 1994, McLaren 1995, Shi et al. 2017, Quinn 2021).

In SOFiA, the rescue effect of adaptive plasticity (Windig et al. 2004, Chevin et al. 2010) is expressed as the expansion of the region of existence (where effects of fluctuations on invariants are buffered). In the simulation, the expansion occurred at intermediate time scales because short-term thermal fluctuations were not enough to sustain rapid phenotypic change. Expansions of the space of existence at shorter (or longer) time scales should be based on the concerted action of plastic responses operating at different time scales, i.e. from hardening to long-term acclimation (Donelson et al. 2018). Hence, the simulation shows that a better understanding of the responses to fluctuations requires models of the 'dynamics' of the formation of the phenotype, which instead will depend on the scale-dependent plastic response. Such models require experiments quantifying how the rate of phenotypic change that is experienced by an organism is driven by temperature; central to such research are time-keeping mechanisms (Giménez et al. 2022) and metabolic rates (Jackson et al. 2021).

An important point in SOFiA is to differentiate between invariants (e.g. body mass) and rates (e.g. growth or sensitivity). Rates capture the relative aspect of the 'effect' of a fluctuation on the invariant because they depend on the reference frame. Hence, SOFiA introduces a level of 'relativism' in the nature of the responses to stressors. This is particularly important when more than one stressor is considered. In such a case, the type of frame (intrinsic or extrinsic) determines the nature of the interactive effect of 2 stressors on an invariant response (Giménez et al. 2022). An important example concerns the combined effect of increased temperature and a second environmental variable. For instance, because temperature increases metabolic demands, increased temperature can exacerbate the negative effect of food limitation on body reserves to metamorphosis (Torres & Giménez 2020). In addition, increased temperature can either mitigate or exacerbate the effect of reduced salinity on survival to metamorphosis (Torres et al. 2021). Importantly, because thermal fluctuations drive developmental rates, the magnitude of body size responses can only be expressed as relative to the reference frame used to measure time. The relativism introduced here has implications for multiple-stressor research; for instance, additive effects relative to clock time will become interactive in biological time (Giménez et al. 2022). Multiple-stressor research has been motivated by the recognition that climate change affects several environmental variables at a time (Gunderson et al. 2016, Boyd et al. 2018). An important objective of this field involves the quantification of the frequency of occurrence of the different types of interactive effects and in which context a stressor mitigates or enhances the effect of another stressor. The fact that the nature of the multiple-stressor effect can depend on the reference frame highlights the need to be clear about what the relevant frame is needed to address a given question.

It can be argued that SOFiA is a general approach in the following sense. First, it can be applied in situations in which biological time and tolerance do not depend on the fluctuations or to more complex experimental designs. If biological time and tolerance do not depend on the fluctuation, the partial differential Eq. (2) simplifies such that the matrix $\boldsymbol{M}$ contains zeros in the off-diagonal entries (μ and τ become linearly related to m and t, respectively) and the response is projected on 2D flat time slices (Fig. 3) at both clock and biological time. Second, given a single variable (e.g. temperature), one can apply this approach to experiments exploring the effect of consecutive waves on biological variable responses by adding a component (to the space of fluctuations) quantifying the time lag between waves (called, respectively, l and λ in the extrinsic and intrinsic frames). Third, one can accommodate additional variables (e.g. food availability, salinity, pCO_2) and the time lag among them in order to explore the effect of simultaneous versus sequential stressor effects (Gunderson et al. 2016). As the level of complexity increases, the limitations are logistical; however, in such a case, one could use information from previous experiments and the mathematical formalism to determine which region of the space of fluctuations should be further explored through a new experiment. Fourth, SOFiA can be applied beyond the organis-

mal level, if one can define metrics for biological times and tolerance (discussion below).

A potential application concerns the species level, where tolerance may be defined as the thermal range that enables a positive population growth rate (Gvoždík 2018) and biological time is defined as the generation time. Given 2 species, we have species-specific biological time scales (τ_1, τ_2) and amplitudes (μ_1, μ_2). In the *mt*-projection, the area where both μ_1 and μ_2 are >1 are regions of extinction for both species. The regions where only one of them is >1 shows the extinction of only one such species; interactions such as symbiosis would be reflected as $\mu_1 = \mu_2$. Areas where any $\mu_i > 1$ indicate conditions leading to environmental filtering (Kraft et al. 2015) in which temperature selects for species assemblages characterised by specific trait combinations. How the $\mu_i = 1$ curves are positioned with respect to $\tau_i = 1$ curves will define regions where extreme fluctuations are longer or shorter than the generation times. Theory (Romero-Mujalli et al. 2021) predicts that the threshold of $\tau = 1$ is important for how adaptive plasticity responds to fluctuations over long time scales.

Portfolio effects (Schindler et al. 2015), driven by phenotypic plasticity and genetic diversity, buffer populations from environmental fluctuations. Portfolio effects should result in patterns analogous to those of Fig. 8, which contrast those shown in Fig. 7. There are also outcomes that depend on the type of interaction. In the case of competition, relative nonlinearity and storage effects maintain coexistence under environmental fluctuations (Descamps-Julien & Gonzalez 2005, Chesson 2018); fluctuations of sufficiently low amplitude should result in competitive exclusion unless fluctuation-independent mechanisms operate. Fluctuation-dependent mechanisms may be reflected in μ-values if 'tolerance' is quantified considering the outcome of species interactions.

The second case concerns biodiversity and ecosystem function (García et al. 2018), in which the invariant function would be biomass or the amount of habitat produced by a foundation species. Examples are macroalgal or mussel beds and coral reefs sustaining function in association with its biomass or canopy. Increases in temperature lead to e.g. coral bleaching (Pratchett et al. 2008). Here, the curve $\tau = 1$ would represent fluctuations occurring at the time scale of the species replacement (i.e. a metric of biological time unit at the level of community; Ontiveros et al. 2021). Community tolerance is defined from the sensitivity of species richness to changes in the time scale of the fluctuation. By moving along the line of $\mu = 1$, we can identify the set of environmental fluctuations driving extinction and collapsing the function. The absence of buffering mechanisms should result in patterns like those in Fig. 7. Buffer effects (as plasticity in Fig. 8) will reflect phenotypic plasticity, portfolio or storage effects. In addition, at this level, species complementarity should also operate as a buffer; species complementarity can sustain function in scenarios of increased temperature (García et al. 2018).

In synthesis, SOFiA could help us to advance our understanding and to predict the effects of environmental fluctuations on biological systems. This is achieved through the synthesis, organisation, and re-interpretation of current information about the effects of environmental fluctuations on tolerance, biological time and chosen 'invariant' responses. As a perspective, SOFiA offers a route for future research, combining mathematical analysis, simulations, and experiments (manipulating fluctuation components), which are then integrated into a wider research programme.

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