Why the architecture of environmental fluctuation matters for fitness

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Abstract

The physical environment represents the very stage upon which the eco-evolutionary play unfolds. How fluctuations in the environment affect fitness is thus central to demographic projections, selection predictions, life history analyses, and conservation of populations. Here we systematically compare and explain why different 'architectures' of fluctuations—both in how they are generated in nature and constructed theoretically—alter fitness. Modelling efforts have mostly characterized variable environments with stochasticity. However, stochasticity refers to a random process. Many fluctuating environments in nature are non-random, driven by geophysical forces that create feedbacks or cyclicality: for example, seasons, tides, day/night, and disturbances such as floods, fires, and hurricanes. We show that evolutionary fitness $log\lambda_s$ of a simple structured population is sensitive to the nature of fluctuations, even if different fluctuations appear indistinguishable in long-run statistical distributions. Importantly, we uncover two mathematical explanations of why fitness depends on the architecture of environmental fluctuations—consecutiveness of deviations from the environmental mean, and Jensen's Inequality acting on nonlinear biological parameters—both arguably relevant features in virtually all populations inhabiting variable environments. The fitness divergence we demonstrate and explain is a useful step towards developing evolutionary demographic theory for the prevalent categories of non-random environments.

Introduction

Predicting population growth—or fitness—is a centerpiece of life history theory, evolutionary demography, and conservation biology. Cole (1954) first conceived of the fitness of life history strategies as directly linked to the strategies' influence on population growth rate. Variations in the age distribution of survival and reproduction shape the fitness landscapes of life histories (Gadgil & Bossert 1970; Stearns 1976), upon which natural selection can act. Classical demography (Keyfitz 1968; Caswell 2001) leverages these concepts to analyze how the trajectories and sensitivities of population growth are influenced by population structures (*e.g.* in age, stage, or size) and their variations.

Early theories began with assumptions of constant environments for simplicity, and because it was necessary to lay the groundwork for comparing species in a systematic manner (Fisher 1958; MacArthur 1962). Developments since (Levins 1968; Schaffer 1974) have largely focused on extending analyses to include stochastic environment assumptions to reflect the complexities of nature (Lande *et al.* 2003; Tuljapurkar *et al.* 2003), and to turn our attention to increasing environmental variability under climate change (Easterling *et al.* 2000; Drake 2005; Boyce *et al.* 2006; Morris *et al.* 2008; Lawson *et al.* 2015). Seminal work by Tuljapurkar *et al.* (2009) demonstrated how and why the expected optimal life histories differ between constant and stochastic environments in a general sense.

In ecology and evolution, stochastic environmental formulations are now so commonplace that the term 'stochastic' is often used interchangeably with 'fluctuating' or 'variable' environments. Stochasticity indeed offers a powerful suite of tools to model an extensive spectrum of environments, principally afforded by mature statistical theories of probability distributions. In

short, a variable environment can typically be statistically summarized with moments of distributions, e.g. the mean ($\bar{x}$) and standard deviation (σ) of a normal or lognormal distribution, derivations of which lead to tractable analytical solutions for biological predictions in that environment (Lawson *et al.* 2015), *e.g.* bet-hedging strategies (Cohen 1966; Childs *et al.* 2010). Higher order moments of stochastic environments can be decomposed with Taylor expansion methods to analyze the effects of, for example, intra- and inter-annual variability and temporal autocorrelation on fitness (Tuljapurkar *et al.* 2009). Indeed, there is substantial theoretical and empirical evidence that 'color' of noise in stochastic environments (negative to zero to positive autocorrelation) influences fitness and extinction risk (Cohen 1966; Lande & Orzack 1988; Vasseur & Yodzis 2004; Halley 2005; Tuljapurkar & Haridas 2006; Reuman *et al.* 2008; Engen *et al.* 2013; Chevin *et al.* 2017). In summary, modern 'stochastic demography' is now a rich discipline that places stochastic environmental formulation at its core to ask ecological and evolutionary questions (Fieberg & Ellner 2001; Engen *et al.* 2009; Tuljapurkar 2013; Chevin *et al.* 2017; Lande *et al.* 2017; Crewe *et al.* 2018; Schreiber & Moore 2018; Davison *et al.* 2019). Mathematically, however, stochasticity is specific: it describes a random process, usually implemented in biological models with stationary probability distributions.

Vast categories of environments are non-randomly driven by external forces in nature. For example, fundamental geophysical fixtures such as the rotation of Earth (governing diel cycles), its axial tilt and revolution around the Sun (seasonal cycles), and the revolution of the Moon around Earth (tidal cycles) set sinusoidal oscillations in most terrestrial and aquatic ecosystems around the planet. Physical processes such as the large mass and heat capacity of deep ocean waters moderating the short-term fluctuations in ocean surface temperatures buffer chance events over time and cause temporal autocorrelation (Steele 1985). Distinct from stochastic variability,

geophysically-driven fluctuations are 1) not emergent products of ecological and evolutionary dynamics, 2) nor are they causally driven by past environmental states as in Markovian processes or in phenomenologically autocorrelated environments. Analogous to driven harmonic oscillators in physics, many environments are governed by permanent (at least on time scales relevant to ecology and evolution) external drivers of fluctuations.

Here we envision generating functions that produce the timing patterns of events or state-changes in an environment—from purely random to cyclical—to compare four broadly representative architectures of fluctuating environments. Events here represent ecological disturbances (Lytle 2001) such as fires, floods, hurricanes, avalanches, droughts, and heatwaves, or, in seasonal systems, onsets of winter that can largely impede biological activity (Inouye 2008). Stearns (1976, Fig. 7) outlined the possible outcomes of environmental fluctuation frequency and predictability for the age distribution of reproduction. Tuljapurkar (1985) analyzed how the relative scaling between the period of environmental cycles and generation time influences population growth rate. Recent theoretical work demonstrated that environmental periodicity is a distinct selective force that determines optimal (Park 2019) as well as individual variation in life histories (Park & Wootton 2021). Further, perturbations to seasonality and disturbance regimes constitute some of the most widespread signatures of climate change, with far-reaching consequences such as phenological shifts (Walther *et al.* 2002; Westerling *et al.* 2006; Marlon *et al.* 2009). Importantly, frequency and predictability can vary independently in disturbance regimes (Lytle 2001; Lytle *et al.* 2008; Denny *et al.* 2009). Thus, teasing apart the different generating functions of environmental variability—beyond collapsing all environmental variability to stochasticity—is crucial not only for more accurate predictions of population growth (Tuljapurkar & Haridas 2006), but for understanding different causal drivers of population dynamics and life history selection.

Here we demonstrate why long-term fitness differs between stochastic *vs*. non-randomly fluctuating environments. We construct a simple demographic fitness model to be systematically compared across four broadly representative categories of fluctuating environments. We identify two general mathematical mechanisms that cause divergences in fitness estimates across the four categories. The first mechanism involves the pattern of consecutiveness of positive or negative deviations from the mean environment; this pattern depends on the generating functions of fluctuations. The second involves Jensen's Inequality acting on nonlinear life history traits, or vital rates; the prevalence of such nonlinearity in nature is likely universal. Both are very general properties of populations in variable environments, and we reveal how the two operate in concert to drive fitness estimates to diverge from purely stochastic models. Finally, we discuss the general relevance of our findings and identify key theoretical extensions and empirical tests that will be important moving forward.

The generating functions of fluctuating environments

We start by setting up four generating functions of fluctuation in environments (Fig. 1). We mean generating functions in the mathematical sense of rules underlying discrete encodings of infinite series of events on a timeline. For all four generating functions, our focal parameter is the *interval* between events. All four generating functions will have an error term σ, and it will be some proportion of mean interval, both of which will be held constant for systematic comparison. Again, these events represent ecological disturbances, or the onset of winter in seasonal systems with the simplifying assumption that winters are harsh enough to perturb or halt biological activity. For the seasonal case, note that celestial seasons are perfectly periodic, but the meteorological (*e.g.*

temperature, frost) onset of winter and arrival of spring are variable, making the intervening season (the interval) also variable in length ('climatological growing seasons', *sensu* Linderholm 2006).

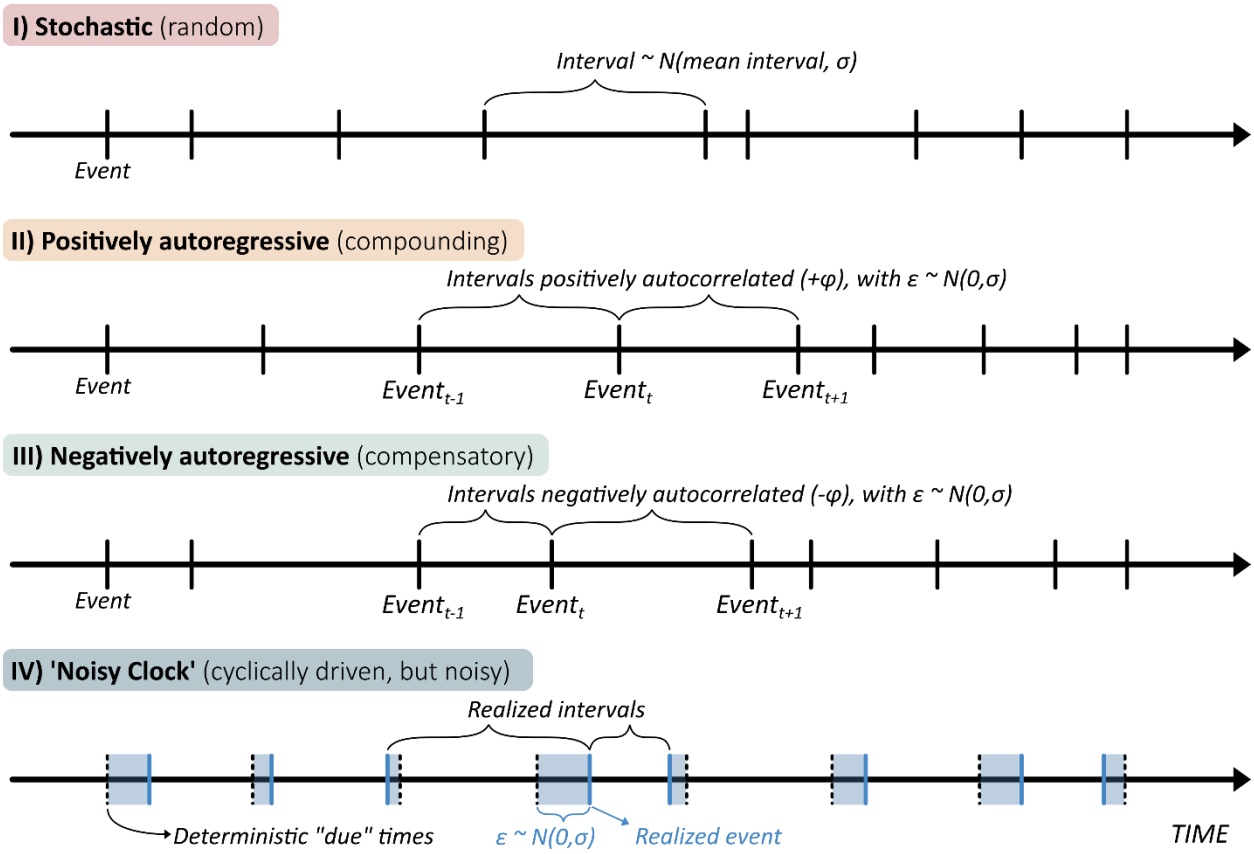

Figure 1. Four generating functions of fluctuating environments. Each fluctuation architecture is determined by the process of generating a sequence of discrete intervals between events on a continuous timeline.

Generating function I: Stochastic (random)

We generate a stochastic environment by drawing event intervals X_t from a normal distribution:

$$X_t \sim N(\bar{X}, \sigma) \tag{1}$$

where $\bar{X}$ is the mean interval. We do this instead of generating a series of events via a Poisson

process, which is a more common way of generating random events on a timeline, to make this case comparable with the other three cases with respect to their error distribution $N(0, \sigma)$, and because in subsequent sections we will manipulate the amount of noise (σ) while holding the mean interval constant (which is not possible with Poisson distributions). Note that this manner of generating a fluctuating environment does not consider the source or nature of the noise, nor the length of preceding intervals (*i.e.,* there is no memory of past fluctuations), but only assumes the long-run statistical distribution of variability. While measured environmental noise may always have a physical source in reality, and all systems may have some memory process to varying degrees, some systems are so complex and noisy that they are well approximated by pure randomness. Stochastic environments are experienced, for example, by mice living in dryland ecosystems with variable resource availability (Noble *et al.* 2019), by weevil species using strongly fluctuating oak acorns as egg-laying sites (Pélisson *et al.* 2012), and by annual herbs growing in or near vernal pools created by stochastic winter precipitation events (Emery & La Rosa 2019).

Generating function II: Positively autoregressive

We generate a positively autocorrelated environment with a simple AR(1) process:

$$X_t = \bar{X} + \varphi X_{t-1} + \varepsilon_t \sim N(0, \sigma) \tag{2}$$

where $\bar{X}$ is the mean interval, and each interval X_t is positively correlated ($+\varphi$) with the interval immediately preceding it (X_{t-1}). The i.i.d. (independent identically distributed) noise ε_t is drawn from $N(0, \sigma)$. Positively autocorrelated environments are characterized by a 'compounding' behavior where a longer or shorter interval than the mean is likely to beget another longer or shorter

interval in the immediate future, respectively. Examples of positively autocorrelated fluctuations in nature include some fire regimes (Caswell & Kaye 2001), oceanic temperatures (Steele 1985; Halley 2005), and flood regimes (Sabo & Post 2008).

Generating function III: Negatively autoregressive

The negative counterpart to the positively autoregressive environment is one with a negative autoregressive term ($-\varphi$) and all other terms identical to Eq. 2:

$$X_t = \bar{X} - \varphi X_{t-1} + \varepsilon_t \sim N(0, \sigma) \tag{3}$$

Negatively autocorrelated environments are characterized by a 'compensating' or self-correcting behavior where a longer or shorter interval than the mean is likely to be counterbalanced with a shorter or longer interval in the immediate future, respectively. Real examples of negatively autocorrelated environments in nature, though much more rarely considered than positively autocorrelated ones (Metcalf & Koons 2007), include terrestrial plant systems with delayed density-dependence driven by nutrient cycling (Gonzalez-Andujar *et al.* 2006), and tree masting (Hacket-Pain & Bogdziewicz 2021).

Generating function IV: 'Noisy Clock'

The last generating function describes a fluctuating environment with a fundamental external driver of cyclicality, whose deterministic periodicity is not affected by the realized noise. We henceforth refer to this case as the 'Noisy Clock' to describe the clocked (deterministic) nature of

fluctuations that underlies the noise. Here, we first punctuate the timeline with a series of deterministic 'due' times of events much like the celestial periodicity of Earth's revolution that determines the boundaries of the annual cycle. Intervals are not generated by counting time from the preceding event, but imperfectly timed events occur around each 'due' time with i.i.d. noise $N(0, \sigma)$. Then the intervals are computed by measuring gaps between subsequent realized events:

$$X_t = Realized\ event_{t+1} - Realized\ event_t$$

$$= [Due_{t+1} + \varepsilon_{t+1} \sim N(0, \sigma)] - [Due_t + \varepsilon_t \sim N(0, \sigma)] \quad (4)$$

Counting time from preceding events (which is the case for generating functions I, II, and III) as opposed to in reference to an external clock would be an unrealistic way to model fundamentally cyclical systems such as seasonal ones. For instance, if one were to model a winter event (*e.g.* first snowfall), but stochastically modelled the length of intervening summer seasons with no regard to due times, then after some additive sequence of stochastic lengths it would be possible to have winters starting in July when lined up against a deterministic calendar. This would be unrealistic under any reasonable geophysical stationarity assumptions. Adding error to due times has the effect of gravitating noisy events back to realistic due times set by the underlying forces of harmonic oscillations in the environment. Real fluctuations with clocked due times driven by geophysical forces—but with error in the measured proxy variables—are exemplified by a myriad of diel (*e.g.* hunting behavior of African wild dogs; Nouvellet *et al.* 2012), tidal (*e.g.* foraging of intertidal snails; Hayford *et al.* 2018), and seasonal environments (*e.g.* advancement of egg-laying with warming springs in numerous bird species; Dunn & Møller 2014). Despite widespread attention to seasonal environments, particularly with respect to global phenological shifts (Walther *et al.* 2002), the theoretical foundation of demographic dynamics and life history evolution in

174 cyclical environments is not yet well understood (Lande *et al.* 2017).

175

176 **Comparing apples to apples: indistinguishable sample distributions**

177 Despite the fact that the four simulated architectures of fluctuation (Fig. 2A) are known *a priori*
178 and fundamentally different, when one samples event intervals from each environmental time
179 series, one recovers normal distributions that are indistinguishable from each other (Fig. 2B&C).
180 The main purpose of demonstrating this sample similarity is to argue that long-run statistical
181 summaries of environments might give, incorrectly, the assurance that one can model any of the
182 four environments stochastically by drawing from the sampled normal distribution. However, we
183 will show shortly that the underlying generating functions, though invisible with sample
184 distributions, change fitness estimates. To our knowledge there is no simple derivation to force the
185 fundamentally different generating functions (Eq. 1-4) to be analytically equivalent with respect
186 to the expected sample distribution. The stochastic case, if generated with the same σ as the other
187 three, produces a slightly narrower sample distribution. We thus applied a multiplier of 1.3 to the
188 σ of the stochastic generating function, which heuristically makes its sample distribution
189 statistically indistinguishable from the other three (Fig. 2C). Our goal was to make the sample
190 distributions as similar as possible to demonstrate in the following steps that, despite their
191 similarity, the unequal architectures of environmental fluctuations produce fitness differences
192 through mechanisms that are invisible from time series summary statistics.

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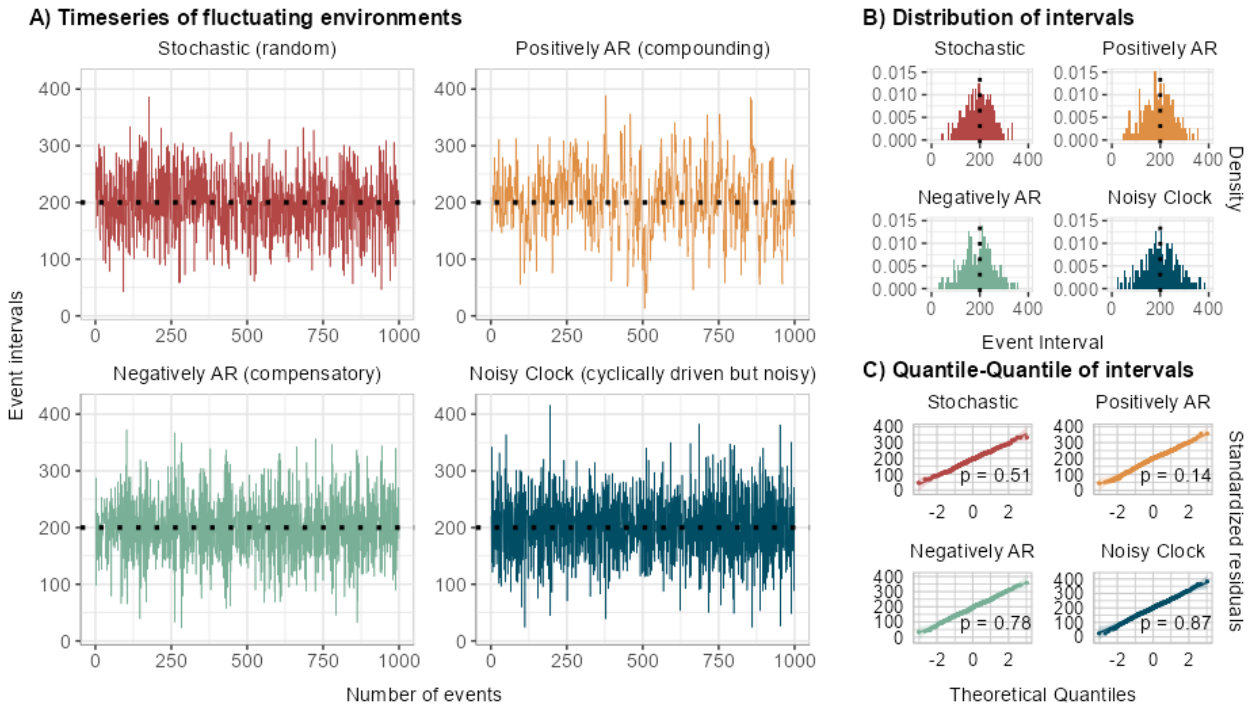

Figure 2. Visualizing the four generated environments. A) Time series of intervals over 1000 events are simulated with $\bar{X} = 200$ and $\sigma = 0.2 \times \bar{X}$. A multiplier of 1.3 was applied to the σ of the stochastic generating function to make the width of all four sample distributions more similar. Dotted lines represent the mean interval. B) Sampling 600 intervals from each environment with replacement recovers normal distributions. Dotted lines represent the mean interval. C) Shapiro-Wilk tests of normality on each independent sample distribution show that all are statistically normal ($p > 0.05$). Further, all six pairwise comparisons between the four sample distributions with Kolmogorov-Smirnov tests show that one cannot reject the null hypothesis that they came from the same distribution (p-value range: 0.15~0.64). AR: autoregressive.

A simple demographic model in fluctuating environments

Upon the environmental fluctuation backgrounds (Fig. 3A), we model a simple population that proceeds through time according to defined life history (or vital) rates. The population, described in a system of discrete difference equations, has a general two-stage structure consisting of juveniles and reproducing adults:

$$\begin{cases} J_{t+1} = A_t f \\ A_{t+1} = A_t S_A + J_t S_J \end{cases} \tag{5}$$

where J_t and A_t are numbers of juveniles and adults at time t respectively, f is adult fecundity, and S_J and S_A are juvenile and adult survival rates respectively. The model is deliberately kept simple in terms of structure for generality, and to focus on the effect that the different generating functions have on fitness. Structural complexity (*e.g*. the number of developmental stages reflected by the number of equations in the system, or the number of relevant vital rate terms) would be an obvious area of customization for system-specific inquiry. As we will show, the important mechanisms should propagate to overall fitness regardless of demographic complexity.

Next, suppose that a vital rate, S_J, changes nonlinearly between events. Verbally, this means that if two disturbance events happen in quick succession, then S_J will be low, and if a long time passes between events, then S_J will be high; and this change in S_J as a function of interval length is nonlinear. For illustrative purposes, we assume the nonlinearity of S_J has a logistic shape as a function of time since last event (Fig. 3B). Biologically, this function signifies the time needed for juveniles to sufficiently develop, grow, or learn to endure the next impending perturbation in the environment. Though not always logistic, nonlinearity in vital rate response functions is likely common (Caswell 2008; Childs *et al.* 2010; Sletvold *et al.* 2013; Taylor *et al.* 2014; Ehrlén *et al.* 2016; Shriver 2016). For example, Morris et al. (2006) showed that, across five species of perennial plants in the USA, vital rates including seedling survival (equivalent to S_J here), survival at other stages, growth, germination, and seed production (equivalent to f here) showed nonlinear change as a function of time since last hurricane or fire disturbance (disturbance phase). Similarly, Bürkli & Jokela (2017) showed that embryonic development success (early-stage juvenile survival) of a freshwater snail changed nonlinearly across the species' reproductive season. The exact shape of vital rate response functions is another key point to be tailored for system-specific inquiry, whether with empirical measurements or as realistic assumptions built into models.

222

223 **Time-averaged fitness varies across the fluctuating environments**

224 For each of the four architectures of environmental fluctuations, we ask what the long-run fitness
225 of a life history would be. The modelled life history is defined as the set of vital rate parameters
226 $\{f, S_A, S_J\}$ in the demographic model, scaled for per time-step rates. We hold $f = 0.2$ and $S_A =$
227 0.95 constant to analyze the effect of fluctuations in S_J along its logistic function about its mean
228 = 0.5 (Fig. 3B). Note that these values are arbitrary but biologically realistic. For fitness, we use
229 the 'small-noise approximation' (Tuljapurkar 1982) of time-averaged fitness in variable
230 environments:

$$log\lambda_s = \lim_{t\to\infty}\left(\frac{1}{t}\right) log[N(t)/N(0)] \tag{6}$$

231 which gives the long-run growth rate in fluctuating environments (also known as 'a') where $N(t)$
232 is the total population size consisting of the sum of both juvenile and adult stages at time t. This
233 metric can be computed from numerical simulations over a long time course of the environment
234 (Caswell 2001), and is a robust approximation of fitness even under considerably large fluctuations
235 (Lande *et al.* 2003; Tuljapurkar *et al.* 2003, 2009). We simulate demographic dynamics (Eq. 5) in
236 each fluctuating environment (Fig. 1) for 1000 event intervals, calculate $log\lambda_s$, and repeat these
237 calculations over 500 iterations. Lastly, we compute all of the above across a spectrum of the
238 generating σ [0,0.3], *i.e.,* the error proportional to mean interval $\bar{X}$, to assess how the amount of
239 fluctuation noise affects the divergence of fitness estimates among the four architectures.

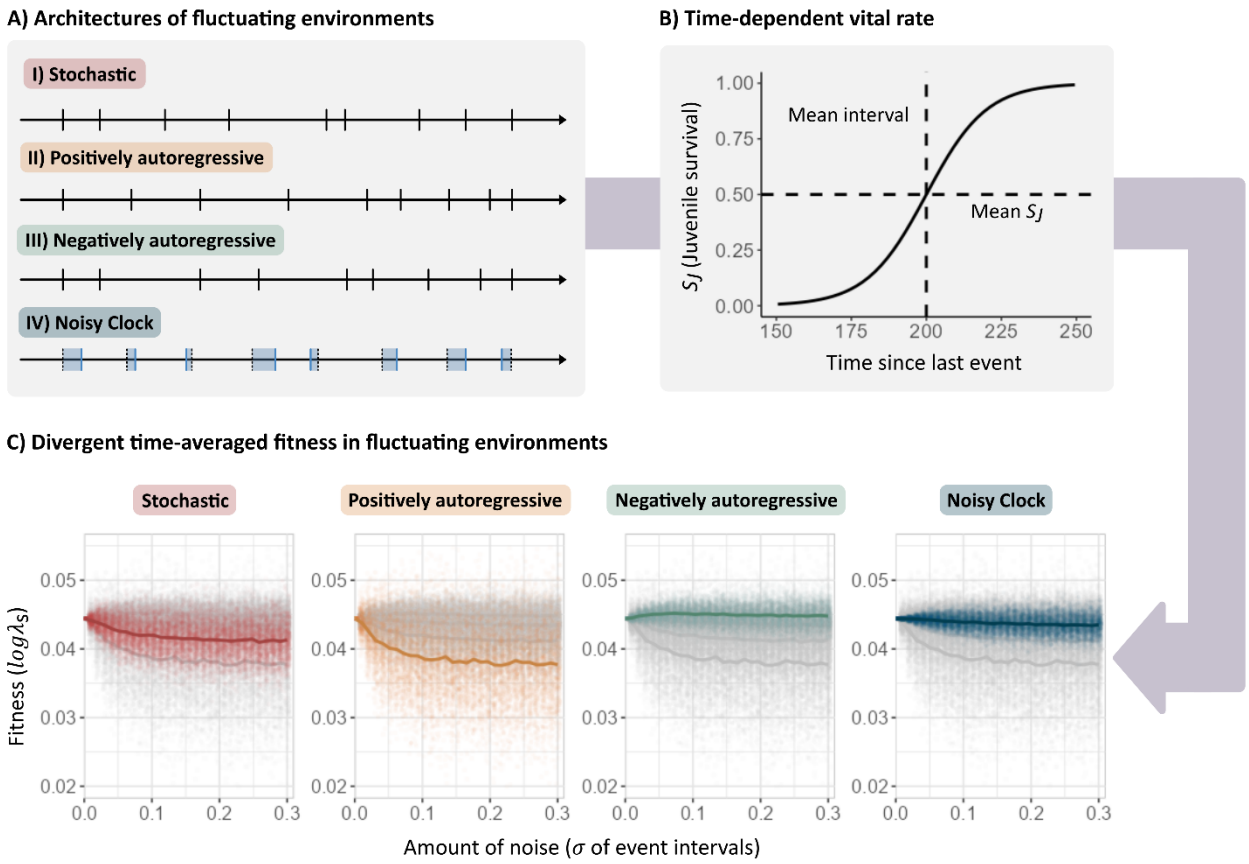

Figure 3. The interaction of environmental fluctuation architecture and nonlinearity in a vital rate creates divergence in fitness estimates. A) Diagrammatic representation of the four architectures of fluctuation. B) Nonlinear response function of a vital rate relative to time since last event. Here, juvenile survival rate (S_J) increases nonlinearly as the length of the interval between subsequent disturbance events increases. Dashed lines indicate the mean*s* of each axis, held constant in all modelled environments. C) Time-averaged fitness estimate*s* ($log\lambda_s$) are driven apart by the generating functions of environmental fluctuations as the amount of noise, or predictability, in the environment increases (modelled with standard deviation of event intervals). Each colored point depicts a single computation of $log\lambda_s$ after 1000 event intervals, corresponding to a given fluctuating environment and a given value of σ [0, 0.3]. The thicker lines correspond to the means of 500 iterations for each environment. The divergence in fitness estimates is largely consistent over the iterations.

Our results show that fitness estimates of the same life history model differ substantially among the four architectures of fluctuating environments (Fig. 3C), despite the close similarity of the environments' long-term time series statistics (Fig. 2). The long-run growth rate $log\lambda_s$ was overall highest for the negatively autoregressive environment, slightly lower for the cyclically driven but

noisy environment (Noisy Clock), still lower for the purely stochastic, and by far the lowest for the positively autoregressive environment. Mean fitness (thicker lines, Fig. 3C) was roughly inversely correlated with amount of variance (spread of dots, Fig. 3C): the lower the mean, the greater the spread. Furthermore, the four environments exhibited unequal responses of fitness to an increase in σ: while increasing σ had a small positive effect on fitness in the negatively autoregressive and Noisy Clock environments, it caused considerable negative trends of fitness in stochastic and positively autoregressive environments. Importantly, all above differences in fitness among the four environments are revealed as amount of noise (σ of event intervals) is increased. This gradual divergence in fitness occurs up to $\sigma \approx 0.1$, after which it qualitatively stabilizes (*i.e.,* further increase in σ seems to have relatively little effect on fitness across all four environments).

Mechanisms of fitness divergence: Consecutiveness of deviations and Jensen's Inequality

The central question that arises from Fig. 3C is why fitness estimates diverge between the four architectures of fluctuating environments, given that the long-term statistical summaries of the environments were hardly different (Fig. 2). There are two mechanisms that work in concert to drive the divergence: (1) *Consecutiveness in deviations from the environmental mean,* and (2) *Jensen's Inequality in vital rate fluctuations.*

(1) Consecutiveness in deviations from the environmental mean

In fluctuating environments with a mean interval, deviations to one side of the mean interval (*i.e.,* below or above) can have short consecutive runs (*e.g.* flipping equally and quickly between below and above the mean) or long consecutive runs (*e.g.* many deviations below or above the mean in a

row) even if the long-term overall distribution of deviations is normally distributed. The four generating functions have different levels of compounding or compensatory behavior of fluctuations, creating different distributions of consecutiveness (Fig. 4A). For instance, negatively autoregressive and Noisy Clock environments both have a tendency to self-correct deviations back to the mean, driven by the $-\varphi$ in the former, and the deterministic 'due times' in the latter. Thus, the two environments have short tails in their distributions of consecutive deviation length, and higher concentrations of short consecutive runs. In contrast, the positively autoregressive environment by definition tends to repeat deviations to one side of the mean in a compounding manner, resulting in a long tail in its consecutive deviation length distribution. The stochastic environment exhibits an intermediate exponential decay distribution of consecutive deviations.

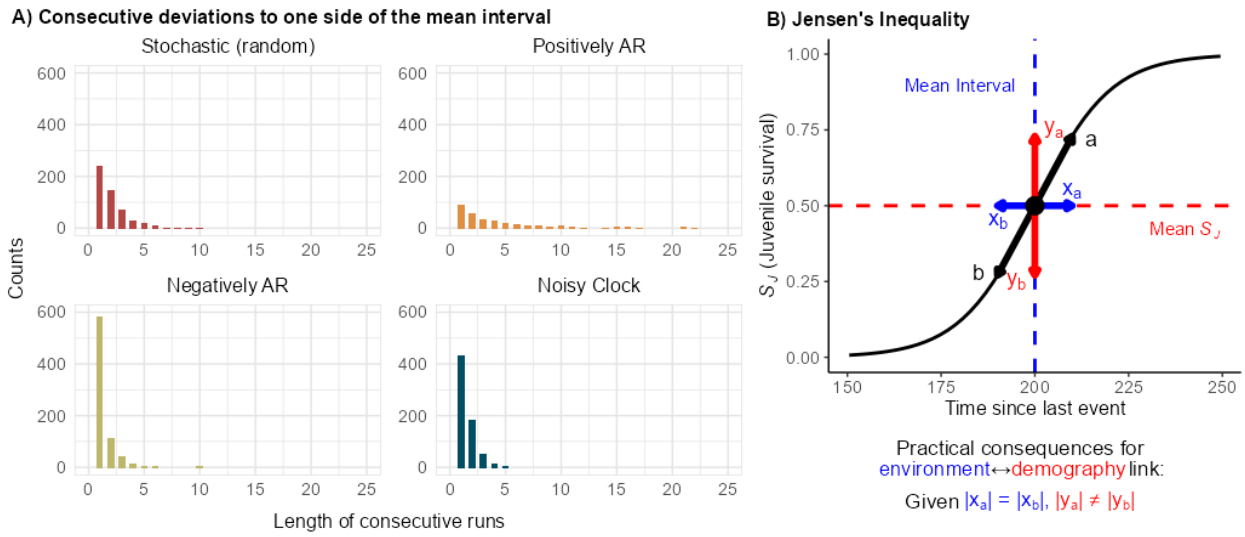

Figure 4. Mechanisms of fitness divergence between the architectures of fluctuating environments. A) Despite very similar long-term distributions of event intervals (Fig. 2), environments have very different distributions of consecutive runs to one side of (below or above) the mean interval depending on the nature of the generating function. Negatively autoregressive and Noisy Clock environments inherently exhibit compensatory or self-correcting behavior, resulting in shorter tails in the consecutive run distribution. The opposite is true of the positively autoregressive case. The stochastic environment exhibits an intermediate exponential distribution. B) Jensen's Inequality exists in any convex/cave fluctuating variable, and introduces asymmetry between environmental and demographic fluctuations. Nonlinear functions in vital rates with respect to intervals between ecological events such as disturbances are likely common. AR: autoregressive.

(2) Jensen's Inequality in vital rate fluctuations

Deviations in the environmental fluctuations below and above the mean interval have asymmetrical consequences for the corresponding nonlinear demographic parameter (*i.e.,* vital rate, here the juvenile survival rate S_J). This asymmetry is referred to as Jensen's Inequality (Jensen 1906; Ruel & Ayres 1999), which states that for a convex or concave function $f(x)$, the average of the function, $\overline{f(x)}$, does not equal the function of the average, $f(\bar{x})$. Verbally, this means that symmetrical fluctuation about the mean of a variable x along the x-axis does not translate equivalently to symmetrical fluctuation about the mean along the y-axis. If we take fluctuation on the x-axis as that of the environment, and fluctuation on the y-axis as that of demography, Jensen's Inequality introduces a break in the environment-demography link in fluctuating environments (Fig. 4B). The direction of that asymmetry (*i.e.,* $f(\bar{x}) \leq or \geq \overline{f(x)}$) as well as its magnitude depend on the convex/cavity of the region of the nonlinear function where the mean lies. Here that nonlinearly fluctuating variable is juvenile survival S_J, which has a direct effect on fitness $log\lambda_s$.

In summary, the mechanisms of fitness divergence between the architectures operate as follows:

i) generating functions cause inherent differences in patterns of consecutive environmental deviations towards one side of the mean, and
ii) since S_J is asymmetrically affected by environmental deviations to one or the other side of the mean due to Jensen's Inequality, time-averaged fitness diverges between environments.

One last element that amplifies the fitness differences further is that $log\lambda_s$ is a multiplicative, or geometric, fitness measure. In other words, short-term fitness differences caused by asymmetric deviations per event are multiplied over the long-run, thus magnifying the divergences.

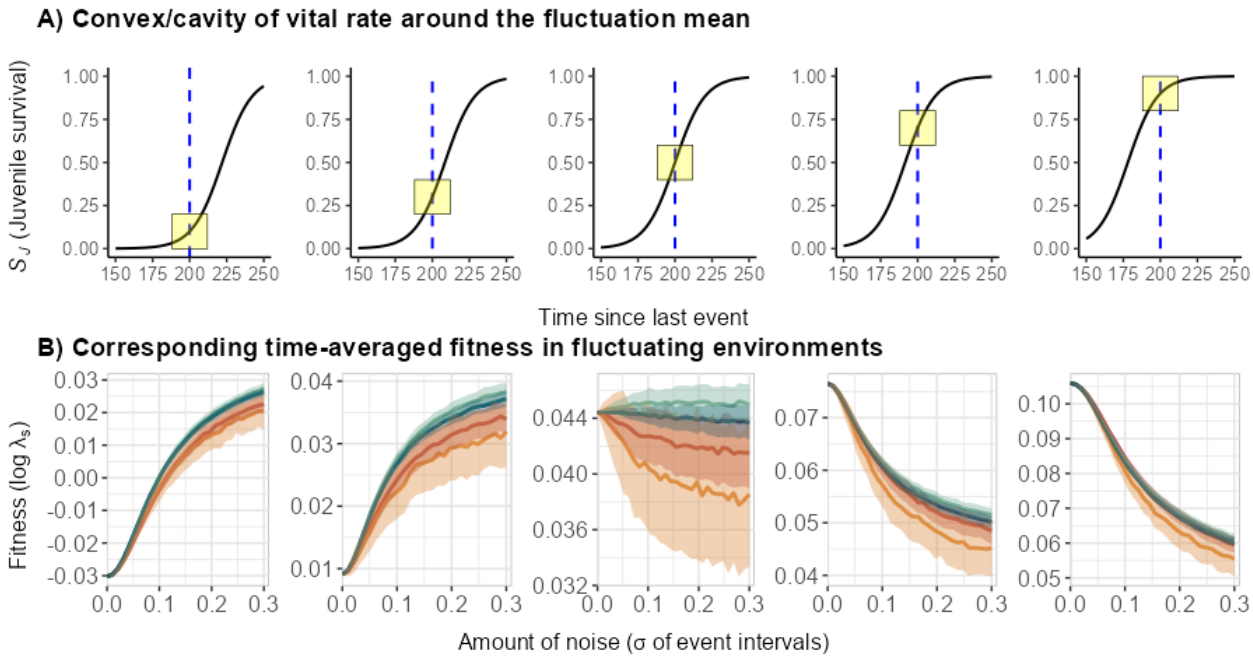

Figure 5. Demonstration of the effect of Jensen's Inequality on fitness divergence across architectures of environmental fluctuation. A) We morph the response function of S_J to manipulate its nonlinear shape around the mean event interval (dashed blue line), which is held constant. Going from left to right, the response function is more convex to more concave around the mean interval, highlighted in the yellow rectangles. This flips the sign of Jensen's Inequality, so that the overall effect of environmental fluctuations on fitness would generally become more positive to negative. B) The corresponding fitness plots demonstrate the sign flip in the effect of Jensen's Inequality as a result of the convex/cavity around the mean. Thick lines are means over all iterations, and bands are ± 1 sd. Colors correspond to the four architectures in previous figures. The middle panel is equivalent to a composite of Fig. 3C.

By manipulating the convex/cavity of the nonlinear demographic parameter S_J around the mean (Fig. 5A), we explore further the biological consequences of the two interacting mathematical mechanisms. When mean juvenile survival is low and its response function convex around the mean (Fig. 5A, left panel), fitness increases with an increase in environmental variability (σ) due to Jensen's Inequality (corresponding panel in Fig. 5B). Conversely, when mean juvenile survival is high and its response function concave around the mean (Fig. 5A, right panel), fitness on average is pulled down with an increase in environmental variability for the same reason (corresponding panel in Fig. 5B). Across the convex/cavity spectrum of the logistic response function of juvenile

survival, as σ of the environmental fluctuation is increased from $0 \rightarrow 0.3$ ($0 \rightarrow 60$ time-steps, since σ is proportional to mean interval = 200), the range of fitness estimates begins to converge for all four environments ($log\lambda_s = 0.02{\sim}0.05$; Fig. 5B, note different y-axis ranges); this occurs because with higher variance, fluctuations begin to sample from wider breadths of the logistic response function which has a combination of convex and concave regions, rendering the role of Jensen's Inequality weaker. Nevertheless, the relative ordering of fitness across environments (Fig. 5B, all panels) remains stable, demonstrating the interactive role that the consecutive deviation patterns of environmental fluctuation architectures (mechanism 1) and the geometric nature of $log\lambda_s$ play in differentiating fitness.

Summary and Future Outlook

We show in this Perspective how relying on simple stochastic modelling to describe fluctuating environments, while powerful, can give erroneous and unreliable estimates of life history fitness in non-randomly fluctuating environments. *A priori* knowledge or quantitative characterization of the nature of fluctuations can thus help us explain a greater breadth of population dynamics and evolutionary trajectories of life histories across environments. Non-random fluctuations abound in nature, from temporally autocorrelated to externally driven cycles (Sabo & Post 2008; Dunn & Møller 2014; Hacket-Pain & Bogdziewicz 2021). Incorporating non-randomness in environmental models is not new to many researchers working on life history theory or demography. Developments in periodic matrix models (Caswell & Trevisan 1994), the seasonal forcing of disease dynamics (Altizer *et al.* 2006), bet-hedging strategies (Venable 2007), and the effect of temporal autocorrelation on life history evolution and population persistence (Pike *et al.* 2004;

326 Metcalf & Koons 2007) are just a few of the examples. The novelty of our results is two-fold: we
327 show for the first time that a systematic comparison of random and non-random fluctuations
328 reveals consistent differences in fitness estimates of a life history; then, we resolve two simple
329 mathematical mechanisms that drive this divergence in fitness. These features are prevalent, and
330 their treatment should open new doors for investigating the implications for demography and
331 selection dynamics in the diverse—and changing—fluctuation architectures in nature.

332 In reality, environmental fluctuations will seldom neatly fall into only one of the architectural
333 categories simulated here. For example, a coastal system that is strongly perturbed by periodic
334 tidal disturbances will also be controlled by a lower resonance of seasonal fluctuations (Denny *et*
335 *al.* 2009). How resonances of non-random fluctuations constructively or destructively interfere to
336 produce a variety of fluctuation superpositions in different ecosystems might explain a wider
337 breadth of observed life history diversity and population trajectories. Even if an environment is
338 predominantly driven by one type of fluctuation architecture, the similarity of the sample
339 distributions (Fig. 2) can make it difficult to unequivocally place a given environment into one
340 fluctuation category. Empiricists could consider plotting the distribution of consecutive deviations
341 relative to a long-term mean interval of events—or periodicity of fluctuation—as we did in Fig.
342 4A. The shape of this distribution, particularly compared against the null hypothesis of a stochastic
343 (purely random) distribution of consecutive deviations simulated with the measured long-term
344 mean and standard deviation, might give an indication of whether an environment is fluctuating
345 positively autoregressively (long tail), or negatively autoregressively / in a Noisy Clock fashion
346 (short tail). Climate scientists and population ecologists regularly use spectral analyses to detect
347 dominant periodicities and lag times in time series of disturbance events or continuous
348 environmental variables (Priestley 1981; Chatfield 2003; Sabo & Post 2008), though often to

remove temporal autocorrelation so long-term trends can be detected (Pyper & Peterman 1998; Brown *et al.* 2011). We argue that consideration of such methods should become more common for life history and evolutionary demography analyses in nature. Our demonstrations suggest that interactions between the architecture of environmental fluctuation and nonlinear biological vital rates (*e.g.* survival, growth, reproduction) will alter fitness estimates in a broad range of situations.

For generality, we strived to simplify our assumptions and structure of the modelling framework, particularly with respect to life history complexity. We emphasize that these are likely fruitful areas for expansion and customization for specific empirical tests. For instance, many species are naturally structured into more than two stages, for example amphibians (*e.g.* egg, larva, adult) and insects (*e.g.* egg, nymph, pupa, adult). The number and interconnectedness of life stages via growth, survival, and reproduction might have other complex and interesting influences on how fitness differs between fluctuation architectures. The nonlinear response function of a vital rate can take many different shapes depending on the more proximate developmental, physiological, or behavioral mechanisms, from quadratic to self-excitatory threshold to polynomial functions (Ellis & Post 2004; Stenseth *et al.* 2004; Nevoux *et al.* 2008). However, regardless of the life history complexity or functional response shape, the joint effect of the two mechanisms we elucidated here (consecutive patterns in fluctuations and Jensen's Inequality) must be in play if there is any nonlinear fitness-related vital rate at any life history stage. If so, the effect should propagate through the entire population dynamic, influence fitness, and drive apart fitness estimates in the different architectures of environmental fluctuations as noise or unpredictability increases. What would vary between systems is the magnitude of that effect depending on how nonlinear the vital rates are, and how sensitive fitness is to those vital rates. Another open question is if interactions between multiple nonlinear vital rates would amplify or dampen the effect of the mechanisms, to

exacerbate or lessen fitness differences between environmental fluctuation architectures.

Perturbation events or periods of harsh conditions are often stark enough to justify focusing on the discrete intervals between them, as we did here, and as is common in disturbance ecology. However, the amplitude, or magnitude, of a continuous environmental variable can itself fluctuate. A prominent example is temperature variability, which is of particular interest in the context of climate change (Post & Stenseth 1999; AghaKouchak *et al.* 2020). In the theoretical framework we present (Fig. 1), variable amplitude can be simulated by allowing the magnitudes of subsequent events to vary randomly or non-randomly, for example in the way events incur mortality or influence the nonlinear vital rate response function following each event. Such analyses might bridge the modelling philosophies that focus on refractory periods between events such as temperature extremes and those that focus on continuous fluctuations in such variables.

Our general conclusion is that careful and appropriate treatments of the generating processes of environmental fluctuations matter for estimating demographic fitness. In conjunction, while nonlinear change in vital rates within seasons or disturbance phases might be arduous to measure given the temporal sampling required, we argue that more often than not linearity is an assumption made for simplicity, not inspired by nature. At least slight nonlinearity is likely a dominant feature of many vital rates, and even if relatively weak, nonlinearity should unlock the synergistic role of the mechanisms discussed here (consecutiveness of deviation patterns, and Jensen's Inequality) to drive differences in fitness estimates depending on the architecture of an environment's temporal fluctuations. Such analyses might significantly improve—as moving from constant to stochastic assumptions did (Tuljapurkar *et al.* 2009)—our understanding of evolutionary demography based on widespread stochastic assumptions.

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