Why the architecture of environmental fluctuation matters for fitness

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Abstract

The physical environment provides the very stage upon which the eco-evolutionary play unfolds. How environmental fluctuations affect fitness is thus central to demographic projections, selection predictions, life history analyses, and the conservation of populations. Modelling efforts have mostly dealt with fluctuating environments using stochasticity. However, environmental fluctuations in nature are combinations of non-random components and stochastic noise. For example, some fluctuations contain feedbacks (*e.g.* disturbances such as floods, fires, and hurricanes), and others are driven by geophysical forces that create fixed cyclicality (*e.g.* seasonal, tidal, and diel). Here we systematically compare and explain why the 'architecture' of fluctuations—both how they are generated in nature and constructed theoretically—influences fitness of structured populations. Fitness is sensitive to the architectures even if they appear indistinguishable in their long-term statistical distributions. Importantly, we highlight two quantitative mechanisms through which fitness depends on fluctuation architecture—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 and 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 spotlight 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, by decomposing the effects of life history speed, dispersion, and temporal correlation on fitness in the two archetypical environmental formulations.

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 summarized by moments of distributions, *e.g.* the

mean and variance of a normal or lognormal distribution, whose derivations 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, *e.g.*, intra- and inter-annual variability and temporal autocorrelation on fitness (Tuljapurkar et al. 2009). Indeed, there is substantial theoretical and empirical evidence that the 'color' of noise (negative to zero to positive autocorrelation) influences fitness and extinction risk (Cohen 1966; Lande and Orzack 1988; Vasseur and Yodzis 2004; Halley 2005; Tuljapurkar and 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 (Tuljapurkar 1990; Fieberg and Ellner 2001; Engen et al. 2009; Chevin et al. 2017; Lande et al. 2017; Crewe et al. 2018; Schreiber and Moore 2018; Davison et al. 2019). Mathematically, however, stochasticity is specific: it describes a process that can be captured with a random probability distribution.

Yet, many common categories of environmental fluctuations have non-random components. 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. Analogous to driven harmonic oscillators in physics, such environments are governed by permanent (at least on ecological and evolutionary time scales) external drivers of fluctuations. Distinct from stochastic variability, geophysically-driven fluctuations are, due to the external driver, thus not emergent products of the internal ecological and evolutionary dynamics of the system such as in population cycles or ecological succession.

Here we envision four broadly representative architectures of the timing patterns of events in an environment. In all four scenarios, events 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 both optimal (Park 2019) and individual variation in life histories (Park and Wootton 2021). Further, perturbations to seasonality and disturbance regimes are among 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, mean and variability can change independently in disturbance regimes (Lytle 2001; Lytle et al. 2008; Denny et al. 2009), which is a growing focus in climate change biology (Jentsch et al. 2007; IPCC 2012; Thornton et al. 2014). Thus, teasing apart the non-random and random components that constitute environmental variability—instead of collapsing all environmental variability to stochasticity—is crucial not only for more accurate predictions of population growth (Tuljapurkar and Haridas 2006), but for understanding fundamentally different causal drivers of population dynamics and life history selection.

We investigate why long-run fitness differs between stochastic *vs*. non-randomly fluctuating environments in a general sense. A particularly novel consideration is the treatment of inherently periodic environments such as seasonal or tidal ones. These externally driven cycles with fixed periodicity are fundamentally different in their memory process compared to internally produced

cycles (*e.g.* autocorrelated): in the former, environmental states gravitate to an external schedule, whereas in the latter they depend on former states of themselves. We systematically demonstrate that this difference translates to consistent fitness differences. We identify two general quantitative 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 arises from 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 elucidate how they 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 environmental fluctuations (Fig. 1): stochastic ("white noise"), positively autoregressive ("red noise"), negatively autoregressive ("blue noise"), and periodic. We mean generating functions in the mathematical sense of rules underlying discrete encodings of sequences of events on a timeline. For all four generating functions, our focal parameter τ_i is the *interval* between events. Again, these events represent ecological disturbances such as fires, or the onset of winter in seasonal systems with the simplifying assumption that winters are harsh enough to perturb or halt biological activity. In seasonal systems, 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 warm season (the interval) also

variable in length ('climatological growing seasons', *sensu* Linderholm 2006). We derive the mean and variance of interval distributions from each generating function to then make them exactly analytically equivalent, before comparing the fitness consequences in environments characterized by the different fluctuations.

Generating function I: Stochastic (random) without feedback

We generate a fluctuating environment with a random sequence of event intervals τ_i:

$$\tau_i \sim Lognormal(\mu, \sigma^2) \quad (1)$$

where μ is the imposed interval mean and σ^2 its variance. 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 distributions and because below we will manipulate the strength of noise (σ^2) while holding the mean interval constant (which is not possible with Poisson distributions because their mean and variance are equal). We use the lognormal distribution because intervals cannot have negative values. 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 (Fig. 1A). While measured environmental variability may in reality always have a physical source, and all systems may have some memory process to varying degrees, some systems are so complex and noisy that they are well approximated by randomness. Random environments may be 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 and La Rosa 2019).

Generating function II: Positively autoregressive

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

$$\tau_i = \mu + \varphi\tau_{i-1} + \varepsilon_i \tag{2}$$

where μ is the desired interval mean, and the interval τ_i is positively correlated by strength of autocorrelation φ with the interval immediately preceding it (τ_{i-1}). The i.i.d. (independent identically distributed) noise ε_i is drawn from $N(0, \sigma_\varepsilon^2)$. 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 (Fig. 1B). Examples of positively autocorrelated fluctuations in nature include some fire regimes (Caswell and Kaye 2001), oceanic temperatures (Steele 1985; Halley 2005), and flood regimes (Sabo and 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:

$$\tau_i = \mu - \varphi\tau_{i-1} + \varepsilon_i \quad (3)$$

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 (Fig. 1C). Real examples of negatively autocorrelated environments in nature, though much more rarely considered than positively autocorrelated ones (Metcalf and Koons 2007), include terrestrial plant systems with delayed density-dependence driven by nutrient cycling (Gonzalez-Andujar et al. 2006), and tree masting (Hacket-Pain and 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. These due times are indexed here by n. 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 (Fig. 1D) Then the intervals are computed by measuring gaps between subsequent realized events:

$$\tau_i = [\mu(i+1) + \varepsilon_{i+1}] - [\mu i + \varepsilon_i] \quad (4)$$

where $\varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ and $i \in \mathbb{Z}_{>0}$, meaning clocked due times are positive integer multiples of μ, the same mean interval as in generating functions I, II, and III. 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 cyclical environments is not yet well understood (Lande et al. 2017).

Comparing apples to apples: equivalent distributions of intervals

To systematically compare the fitness consequences in the four scenarios of fluctuating environments, we take the parametric moments of the generating functions and derive input

parameters that make their interval distributions analytically equivalent (Table 1). All distributions will be normal due to the central limit theorem (Fig. S1). In other words, by using these input parameters all four environments' distributions of intervals will have the same mean and variance, despite the environments' differences in fluctuation architecture. The purpose of establishing this interval distribution equivalency is to demonstrate that long-term statistical summaries of real environments (particularly those coming from sparse data) might lead, incorrectly, to the complacency that one can model any actual environment as a randomly noisy environment that can, consequently be drawn from a random probability distribution. While this simplification might be acceptable in some cases, we will show that long-run fitness is substantially and consistently influenced by the underlying architecture of fluctuations even if their interval distributions are identical.

For our simulations, we set up all four generating functions to have a sample mean interval length (μ_s) of 365 time steps (*i.e.* days) to emulate an annual event process.

A simple demographic model in fluctuating environments

Upon the environmental fluctuation backgrounds that have fundamentally different generating functions but equivalent interval distributions, we model a simple population that proceeds through time. There are two time indices: t which denotes time steps, here representing days, and τ_i which denotes the intervals between intermittent disturbance events set by the generating functions. J_t and A_t are numbers of juveniles and adults at time t respectively, f is rate of reproduction, and S_J [0,1] and S_A [0,1] are rates of juvenile and adult survival when disturbances happen, respectively. The population dynamic is then described in a system of discrete difference equations consisting

209 of juveniles and reproducing adults:

$$J_{t+1} = A_t f$$
$$A_{t+1} = A_t S_A + J_t S_J \,,$$

$$where\ S_J = \begin{cases} S_J(\tau) = \dfrac{1}{1 + e^{-0.1(\tau - 365)}}, & \text{if } t \in y_k = \sum_{i=1}^{k} \tau_i \,, \\ 1, & \text{otherwise} \end{cases} \tag{5}$$

210 We focus on juvenile survival S_J as the vital rate that dynamically interacts with the disturbance
211 events that arrive intermittently into the system. This is because, in many natural populations of
212 plants or animals, juvenile mortality is especially sensitive to harsh environmental conditions
213 (disturbance or winter) (Gaillard et al. 1998, 2000; Higgins et al. 2000; Lytle 2002; McAdam and
214 Boutin 2003; Staver et al. 2009; Park 2019). In Eq 5, juvenile survival S_J is determined by a
215 response function $S_J(\tau)$ when disturbance occurs (*i.e.* when time step t is an element of the
216 predetermined sequence of disturbance timings, which is the cumulative sum of successive interval
217 lengths $\sum_{i=1}^{k} \tau_i$, where k is number of intervals simulated), and is 1 otherwise. Here we have set
218 the response function $S_J(\tau)$ to be a nonlinearly increasing function that depends on how much time
219 has passed since the last event (τ), with juvenile survival being 50% (*i.e.* $S_J = 0.5$) at the mean
220 disturbance interval (Fig. 2B). Verbally, this means that if two disturbance events happen in quick
221 succession, juvenile survival will be low, and if a long time passes between events, it will be high;
222 and this change in juvenile survival as a function of interval length is nonlinear. Biologically, this
223 function signifies the time needed for juveniles to sufficiently develop, grow, or learn to endure
224 the next impending perturbation in the environment. Though not always logistic, nonlinearity in
225 vital rate response functions in between perturbations in the environmental state is likely common
226 (Caswell 2008; Childs et al. 2010; Sletvold et al. 2013; Taylor et al. 2014; Ehrlén et al. 2016;

227 Shriver 2016). For example, Morris et al. (2006) showed that, across five species of perennial
228 plants, vital rates including seedling survival (equivalent to S_J here), survival at other stages,
229 growth, germination, and seed production (equivalent to f here) changed nonlinearly as a function
230 of time since last hurricane or fire disturbance. Similarly, Bürkli & Jokela (2017) showed that
231 embryonic development success (early-stage juvenile survival) of a freshwater snail changed
232 nonlinearly across the species' reproductive season. The exact shape of vital rate response
233 functions is another key point to be tailored for system-specific inquiry, whether with empirical
234 measurements or as realistic assumptions built into models.

235 The model is otherwise kept simple for generality, and to focus on the effect that the different
236 generating functions have on fitness. Structural complexity such as the number of developmental
237 stages (*i.e.* the number of equations in the system, or the number of vital rate terms) would be an
238 obvious area of customization for system-specific inquiry. We also hold f constant at 0.3, and S_A
239 constant at 0.9 when disturbance occurs irrespective of time since last disturbance, and 1 otherwise.
240 These values are arbitrary but biologically realistic; exact values did not influence the downstream
241 qualitative results. As we will show, the important mechanisms should influence fitness regardless
242 of demographic nuance.

243

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

245 Within each of the four architectures of environmental fluctuations, we ask what the long-run
246 fitness of a life history would be. For fitness, we use:

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

247 which gives the long-run growth rate in fluctuating environments (Tuljapurkar 1990) where $N(t)$
248 is the total population size at time *t*, including both juvenile and adult stages. This metric can be
249 computed from numerical simulations over a long time course of the environment (Caswell 2001),
250 and robustly approximates fitness even under considerably large fluctuations (Lande et al. 2003;
251 Tuljapurkar et al. 2003, 2009). We simulate demographic dynamics (Eq. 5) in each fluctuating
252 environment (Fig. 1) for 1000 event intervals, calculate $log_e\lambda_s$, and repeat these calculations over
253 500 iterations. Lastly, we compute all of the above across a spectrum of the generating functions'
254 variance, to assess how the amount of fluctuation noise affects the divergence of fitness estimates.

255 Our results show that fitness estimates of the same life history model differ substantially among
256 the four architectures of fluctuating environments (Fig. 2C), despite the analytical equivalency of
257 the environments' distributions of event intervals (Table 1). The long-run growth rate $log_e\lambda_s$ was
258 overall highest for the negatively autoregressive environment, slightly lower for the cyclically
259 driven but noisy environment (Noisy Clock), still lower for the stochastic environment without
260 autocorrelation, and by far the lowest for the positively autoregressive environment. Mean fitness
261 (thicker lines, Fig. 2C) was roughly inversely correlated with amount of variance (spread of dots,
262 Fig. 2C): the lower the mean, the greater the spread. Furthermore, the four environments exhibited
263 unequal responses of fitness to an increase in the amount of noise (σ^2 of event intervals): while
264 increasing σ^2 slightly increased fitness in the negatively autoregressive and slightly decreased
265 fitness in the Noisy Clock environment, it considerably reduced fitness in stochastic and positively
266 autoregressive environments (Fig. 2C). Importantly, all above differences in fitness among the
267 four environments are amplified as σ^2 is increased. The divergence in fitness also remains largely

unchanged when the rate of reproduction *f* and adult survival S_A are allowed to vary (Fig. S2).

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

The central question that arises from Fig. 2C is why fitness estimates diverge between the four architectures of fluctuating environments, despite the environments' distributions of event intervals being forced to be analytically equivalent (Table 1). There are two mechanisms that work in concert to drive the divergence: (1) *Consecutiveness of deviations from the environmental mean,* and (2) *Jensen's Inequality in vital rate fluctuations.*

(1) Consecutiveness of 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 normal. The four generating functions have different levels of compounding or compensatory behavior of fluctuations, creating different distributions of consecutiveness (Fig. 3A). Negatively autoregressive and Noisy Clock environments both tend to self-correct deviations back to the mean, driven by the $-\varphi$ in the former, and by the deterministic 'due times' in the latter. Thus, these environments have short tails in their distributions of consecutive deviation length. In contrast, the positively autoregressive environment by definition repeats deviations to one side of the mean, resulting in a long tail. The stochastic environment exhibits an intermediate exponential distribution of consecutive deviations.

Why does the distribution shape of consecutive deviations matter for fitness, if over time, there is an identical symmetrical accumulation of negative and positive deviations (*i.e.* normal distribution of intervals; Table 1)? Long-run fitness $log_e\lambda_s$ is a multiplicative, or geometric, fitness measure. Consecutive runs of positive deviations of a vital rate (*e.g.* 'good' years) will never evenly compensate for equally long consecutive runs of negative deviations of the same magnitude (*e.g.* 'bad' years) with respect to population growth (Haccou and Vatutin 2003; Cuddington and Hastings 2016). Therefore, in structured populations, the distribution of the lengths of consecutive deviations should influence long-run fitness (longer tail = lower fitness).

(2) Jensen's Inequality in vital rate fluctuations

Fluctuations below and above the mean interval also have asymmetrical consequences for the corresponding nonlinear demographic parameter; here that parameter is juvenile survival S_J, which has a direct effect on fitness $log_e\lambda_s$. This asymmetry is referred to as Jensen's Inequality (Jensen 1906; Ruel and Ayres 1999), which states that for a convex or concave function $f(x)$, $E[f(x)] \leq or \geq f(E[x])$. Verbally, this means that symmetrical fluctuation of a variable x about its mean along the x-axis does not translate equivalently to symmetrical fluctuation about its mean along the y-axis. If we take fluctuation along the x-axis as that of the environment, and fluctuation along the y-axis as that of demography, Jensen's Inequality introduces a break in the environment-demography link in fluctuating environments (Fig. 3B).

The direction of that asymmetry (*i.e.* sign of the inequality) and its magnitude depend on the convex/cavity of the region of the nonlinear function where the mean lies. We demonstrate the consequence of this dependency by manipulating the convex/cavity of the nonlinear demographic

parameter S_J around the mean (Fig. 4A). When mean juvenile survival is low and its response function convex around the mean (Fig. 4A, panels towards the left), fitness increases with increasing environmental variability σ^2 (corresponding panels in Fig. 4B). Conversely, when mean juvenile survival is high and its response function concave around the mean (Fig. 4A, panels towards the right), fitness curves are pulled down with increasing σ^2. Regardless of the convex/cavity of the response function of juvenile survival, as σ^2 increases fitness curves in all four environments begin to stabilize; this occurs because with higher environmental variance, fluctuations begin to sample from wider breadths of the logistic response function which has a combination of convex and concave regions, weakening the relative role of Jensen's Inequality. Nevertheless, the relative ordering of fitness across fluctuation architectures remains stable (Fig. 4B, all panels), demonstrating the interactive role that the consecutiveness of deviations from the environmental mean and the geometric nature of $log_e\lambda_s$ play in setting the initial divergence of fitness between fluctuation architectures, and maintaining it.

Summary and Future Outlook

Non-random temporal environmental variability abounds in nature, from autocorrelated fluctuations to externally driven cycles (Sabo and Post 2008; Dunn and Møller 2014; Hacket-Pain and Bogdziewicz 2021).Yet the rich diversity of non-random fluctuations is often absorbed into stochasticity (described by random probability distributions) in ecological and evolutionary models, for its alluring mathematical properties and 'good enough' approximations of nature. We have shown that for fitness, the architecture of non-random components of variability matters, even when long-term environmental variabilities are distributed equivalently.

333 In itself, incorporating non-randomness in environmental models is not new to many researchers
334 working on life history theory or demography. Developments in periodic matrix models (Caswell
335 and Trevisan 1994), the seasonal forcing of disease dynamics (Altizer et al. 2006), bet-hedging
336 strategies (Venable 2007), and the effect of temporal autocorrelation on life history evolution and
337 population persistence (Pike et al. 2004; Metcalf and Koons 2007; Tuljapurkar et al. 2009) are just
338 some examples. The novelty of our results is two-fold: we show for the first time that a systematic
339 comparison of random and non-random fluctuations reveals consistent differences in demographic
340 fitness; then, we highlight two simple mechanisms that drive this divergence. These mechanisms
341 are prevalent, and their treatment should open new doors for investigating demography and
342 selection dynamics in the diverse—and changing—fluctuation architectures in nature.

343 Our results corroborate a message that has repeatedly emerged out of the theoretical literature of
344 colored noise and extinction risk, namely that "red" environments (positively autocorrelated)
345 increase extinction risk while "blue" environments (negatively autocorrelated) do the opposite
346 (Lawton 1988; Halley and Kunin 1999; van de Pol et al. 2011; Halley et al. 2018). Although we
347 focused on long-run fitness as opposed to extinction risk *per se,* the link to population persistence
348 is obvious: in positively autocorrelated environments, the long-run growth rate was not only lowest
349 by far, it also showed the highest amount of variance (Fig. 2C), increasing the likelihood of a
350 population crash proving fatal. In contrast, negatively autocorrelated fluctuations led to the highest,
351 most constant long-run fitness (Fig. 2C). Importantly, we further distinguish autocorrelated
352 environments from Noisy Clock environments (*e.g.* seasonal, tidal, and diel). Autocorrelated
353 environments rely on the memory of past events, whereas Noisy Clock environments, in their
354 simplest form, are memoryless and instead anchored to an external clock such as Earth's spin and
355 revolution around the sun. This subtle difference—invisible through distributions of fluctuation

intervals—translates to fundamental differences in the distribution of consecutive deviations from the fluctuation mean (Fig. 3A), and thus long-run fitness. In our simulations, fitness in Noisy Clock environments consistently fell between that of red and blue environments (Figs. 2C & 4B), suggesting that modelling a seasonal environment simply as an autocorrelated one might lead to erroneous calculations of fitness. This result further suggests that Noisy Clock environments, due to their locking onto an external clock, stabilize population growth compared to other types of fluctuations; mathematical proof of this notion would be interesting and broadly relevant as Noisy Clock-like environments are ubiquitous.

In reality, environmental fluctuations will seldom neatly fall into only one of the architectural categories simulated here. For example, a coastal system that is strongly perturbed by periodic tidal disturbances will also be influenced by seasonal fluctuations (Denny et al. 2009). How resonances of non-random fluctuations constructively or destructively interfere to produce a variety of fluctuation superpositions in different ecosystems might explain a wider breadth of observed life history diversity and population trajectories. Even if an environment is predominantly driven by one type of fluctuation architecture, the equivalence of the interval distributions as we showed here can make it difficult to place a given environment into one fluctuation category. Empiricists could consider plotting the distribution of consecutive deviations from the measured mean fluctuation interval, as we did in Fig. 3A. The shape of this distribution, compared against the null of a distribution of consecutive deviations simulated with a purely random fluctuation assumption (Fig. 3A, "stochastic") might give an indication of whether an environment is fluctuating positively autoregressively (long tail in the distribution of consecutive deviations), or negatively autoregressively / in a Noisy Clock fashion (short tail). Climate scientists and population ecologists regularly use spectral analyses to detect dominant periodicities and lag

379 effects in time series of disturbance events or continuous environmental variables (Priestley 1981;
380 Chatfield 2003; Sabo and Post 2008), though often to remove temporal autocorrelation so that
381 long-term trends can be detected (Pyper and Peterman 1998; Brown et al. 2011). We argue that
382 consideration of such methods should become more common for life history and evolutionary
383 demography analyses in nature. Our demonstrations suggest that interactions between the
384 architecture of environmental fluctuation and nonlinear biological vital rates (*e.g.* survival, growth,
385 reproduction) will alter fitness estimates in a broad range of situations.

386 Notably, these fitness differences arise from environmental sensitivity in just one vital rate—
387 juvenile survival—while adult survival and fecundity were modelled as environment-independent.
388 For generality, we strived to simplify our life history model, but its degree of complexity is likely
389 another fruitful avenue of expansion and customization for specific empirical tests. For instance,
390 many species have more than two life stages, for example amphibians (*e.g.* egg, larva, adult) and
391 insects (*e.g.* egg, nymph, pupa, adult). The number and interconnectedness of stages via growth,
392 survival, and reproduction might have other complex and interesting influences on how fitness
393 differs between fluctuation architectures. The nonlinear response function of a vital rate can take
394 many different shapes depending on the proximate developmental, physiological, or behavioral
395 mechanisms, from quadratic to self-excitatory threshold to polynomial functions (Ellis and Post
396 2004; Stenseth et al. 2004; Nevoux et al. 2008). However, regardless of life history complexity or
397 functional response shape, the mechanisms we elucidated here (consecutive patterns in
398 fluctuations and Jensen's Inequality) must be in play if there is any nonlinear fitness-related vital
399 rate at any life history stage. If so, the effect should propagate through the entire population
400 dynamic, influence fitness, and drive apart fitness estimates in the different architectures of
401 environmental fluctuations as variability 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 theory. However, the amplitude, or magnitude, of a continuous environmental variable can itself fluctuate. A prominent example is temperature variability, of particular interest in the context of climate change (Post and 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 two mechanisms discussed here 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 so far largely based on stochastic assumptions.

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Figures & Legends

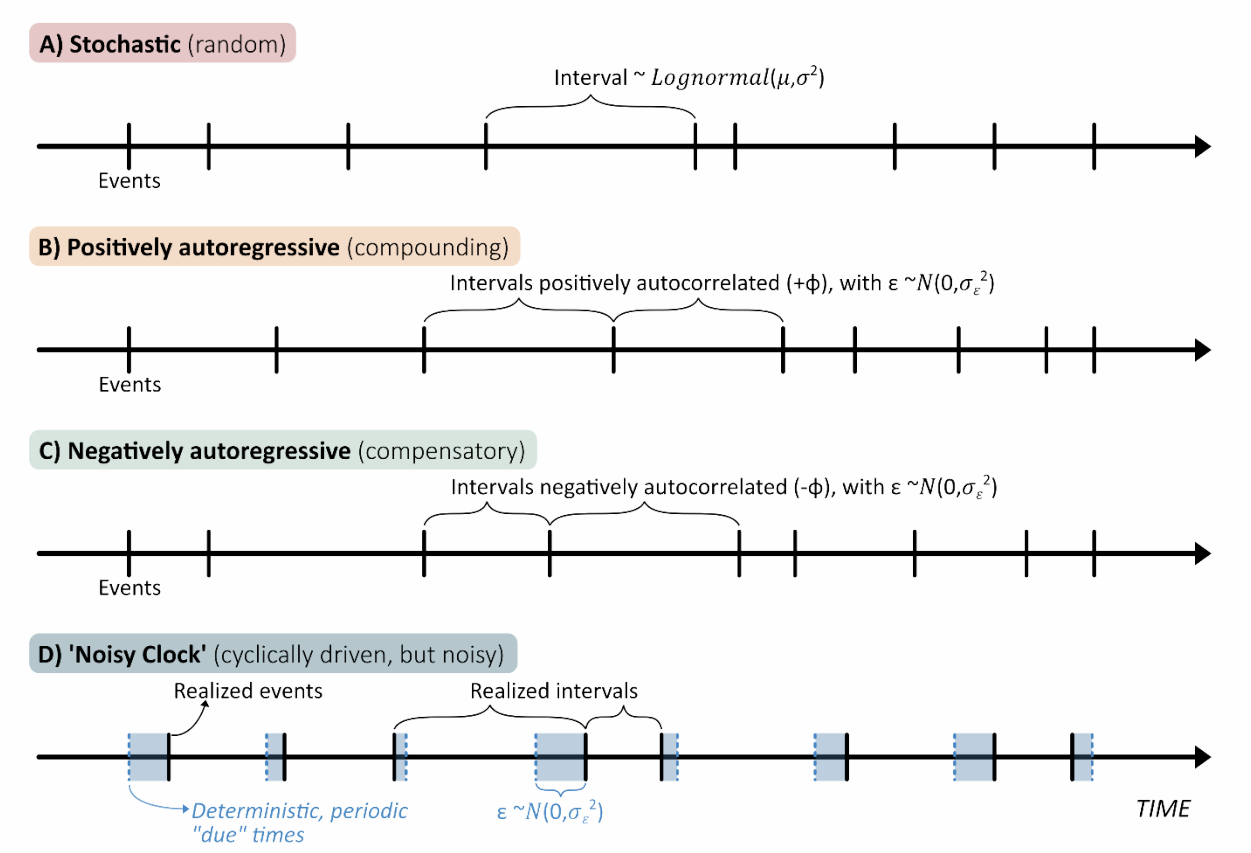

Figure 1. Four generating functions of fluctuating environments. Each fluctuation architecture is simulated by generating a sequence of event intervals on a timeline. Events, denoted by the tick marks, may represent ecological disturbances or winters that bring harsh conditions for biological activity. A) A stochastic environment is generated by drawing a sequence of intervals from a random probability distribution. B) A positively autoregressive environment is generated with positive linear dependency of subsequent intervals on immediately preceding ones (an AR(1) process), with random error; C) the negatively autoregressive environment is only different from B in that the linear dependency on the past interval is negative. D) A Noisy Clock environment assumes a series of unseen "due times" that are perfectly periodic (dashed blue tick marks), but

the actual events occur as a result of error around those due times (blue shaded regions); the gaps between realized events form the sequence of realized intervals.

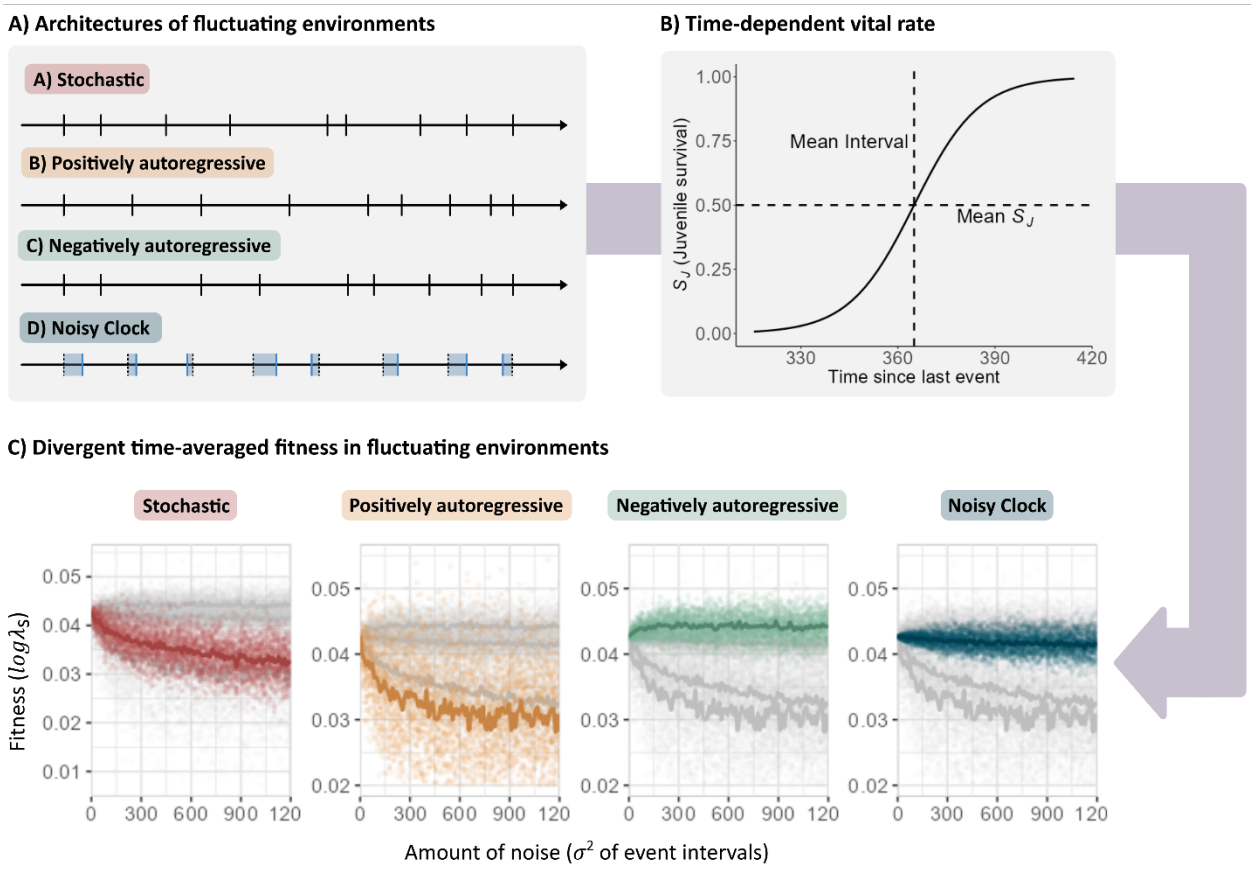

Figure 2. The interaction of environmental fluctuation architecture and nonlinearity in a vital rate creates divergence in fitness estimates. A) Diagrammatic representation of the four architectures of fluctuation, through which the demographic dynamics proceed. B) Nonlinear response function of a vital 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 means of each axis, held constant in all modelled environments. C) Time-averaged fitness estimates ($log_e\lambda_s$) are driven apart by the generating functions of environmental fluctuations as the amount of noise, or unpredictability, in the environment increases (modelled with variance 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 σ^2, with points

corresponding to the other three simulated environments shown in gray for comparison. The thicker lines correspond to the means of 500 iterations for each environment (architecture × noise level). The divergence in fitness estimates is largely consistent over the iterations.

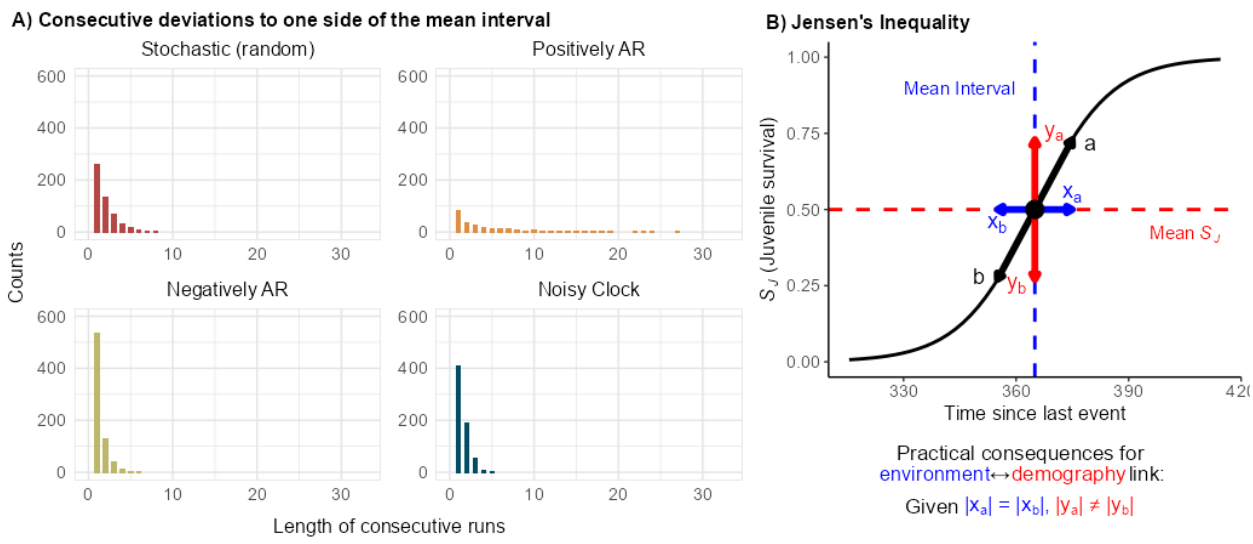

Figure 3. Mechanisms of fitness divergence between the architectures of fluctuating environments. A) Despite analytically equivalent distributions of event intervals (Table 1), environments have very different distributions of consecutive runs to one side of (below or above) the mean interval depending 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.

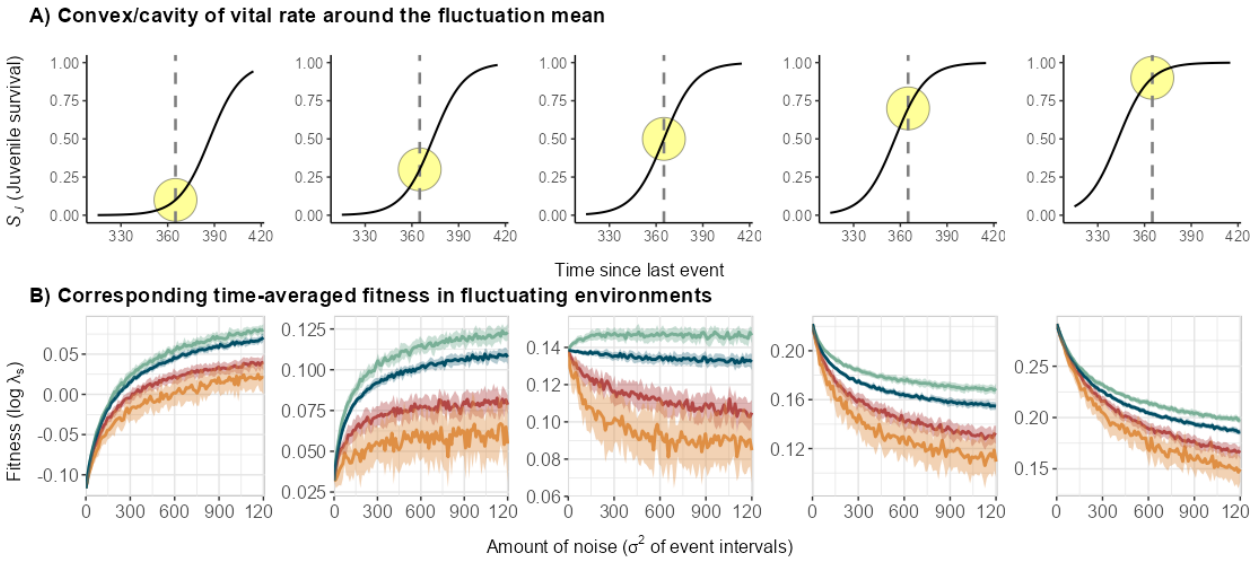

Figure 4. Demonstration of the effect of Jensen's Inequality on fitness divergence across architectures of environmental fluctuation. A) We morph the response function of juvenile survival S_J to manipulate its nonlinear shape around the mean event interval (dashed line), which is held constant. Going from left to right, the response function is more convex to more concave around the mean interval, highlighted in the yellow circles. 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. 2C.

Tables

	Generating Function for interval τ_i	Expected Value	Variance	Generating function parameters in terms of desired sample μ_s and σ_s^2
I	$\boldsymbol{\tau_i} \sim Lognormal(\mu, \sigma^2)$	$E[\tau] = e^{\mu+\frac{1}{2}\sigma^2}$	$Var[\tau] = (e^{\sigma^2} - 1)(e^{2\mu+\sigma^2})$	$\mu = log_e\left(\frac{\mu_s^2}{\sqrt{\mu_s^2 + \sigma_s^2}}\right)$ $\sigma^2 = log_e\left(1 + \frac{\sigma_s^2}{\mu_s^2}\right)$
II	$\boldsymbol{\tau_i} = \mu + \varphi\tau_{i-1} + \varepsilon_i,$ $where\ \varepsilon_i \sim N(0, \sigma_\varepsilon^2)$	$E[\tau] = \mu$	$Var[\tau] = \frac{\sigma_\varepsilon^2}{1 - \varphi^2}$	$\mu = \mu_s$ $\sigma_\varepsilon^2 = \sigma_s^2(1 - \varphi^2)$
III	$\boldsymbol{\tau_i} = \mu - \varphi\tau_{i-1} + \varepsilon_i,$ $where\ \varepsilon_i \sim N(0, \sigma_\varepsilon^2)$	$E[\tau] = \mu$	$Var[\tau] = \frac{\sigma_\varepsilon^2}{1 - \varphi^2}$	$\mu = \mu_s$ $\sigma_\varepsilon^2 = \sigma_s^2(1 - \varphi^2)$
IV	$\boldsymbol{\tau_i} = [\mu(i+1) + \varepsilon_{i+1}] - [\mu i + \varepsilon_i],$ $where\ \varepsilon_i \sim N(0, \sigma_\varepsilon^2)$ and $i \in \mathbb{Z}_{>0}$	$E[\tau] = \mu$	$Var[\tau] = \sigma_\varepsilon^2 + \sigma_\varepsilon^2$	$\mu = \mu_s$ $\sigma_\varepsilon^2 = \frac{1}{2}\sigma_s^2$

Table 1. Expressions of parametric moments of the four generating functions of environmental fluctuations, and the derivations for input moments in terms of the desired (imposed) sample mean and variance to make all distributions analytically equivalent across the four generating functions.