Why the architecture of environmental fluctuation matters for fitness

Article type: Synthesis & Perspective

Short running head: Architecture of fluctuations and fitness

Keywords: fluctuating environments, life history, evolutionary demography, stochastic fitness, nonlinearity, Jensen's Inequality

Data accessibility statement: No new data were used in this study.

Number of words in abstract: 199

Number of words in main text: 5327

Number of figures: 5

Number of tables: 0

Number of text boxes: 0

Number of references: 85

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 terms of 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 quantitative mechanisms through which 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 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 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.

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 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 (Fieberg and Ellner 2001; Engen et al. 2009; Tuljapurkar 2013; 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 random process, usually implemented in biological models with stationary probability distributions.

On the other hand, many common categories of environmental fluctuations in nature are non-random. 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. Analogous to driven harmonic oscillators in physics, such environments are governed by permanent (at least on time scales relevant to ecology and evolution) external drivers of fluctuations. Distinct from stochastic variability, geophysically-driven fluctuations are thus not emergent products of the internal ecological and evolutionary dynamics of the system, due to the external driver. However, non-random fluctuations in the environment

can also be driven by past ecological states within the system in Markovian or "brown" noise fashion (Halley and Kunin 1999), or can occur in in phenomenological cycles (*e.g.* population cycles or ecological succession). Larger scale physical processes with memory of past states such as the vast mass and heat capacity of deep ocean waters moderate the short-term fluctuations in ocean surface temperatures to buffer chance events over time, and cause temporal autocorrelation in temperature (Steele 1985).

Here we envision different generating functions that produce the timing patterns of events or state-changes in an environment, 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 and 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 and Haridas 2006), but for understanding

different causal drivers of population dynamics and life history selection.

Here we investigate why long-term fitness differs between stochastic *vs*. non-randomly fluctuating environments in a general sense. A particularly novel consideration is the treatment of periodic environments (but with natural noise in the periodicity) such as seasonal or tidal ones, which have been commonly dealt with using fixed sinusoidal or wave forcing (Altizer et al. 2006), or autoregressive functions (Stenseth et al. 1998). Externally driven cycles with fixed periodicity such as seasons and tides are inherently different in their memory process compared to internally produced cycles (*e.g.* autocorrelated), and we demonstrate that this difference translates to fitness consequence differences. We simulate a common demographic fitness model across four broadly representative categories of fluctuating environments—stochastic (white noise), positively autocorrelated (red noise), negatively autocorrelated (blue noise), and periodic—with the explicit goal of comparing fitness consequences across them in a systematic fashion. In so doing, 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 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 parameter σ, and it will be some proportion of mean interval, both of which will be held constant across the generating functions 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).

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 variability 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 and 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 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:

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

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

Comparing apples to apples: indistinguishable sample distributions

Despite the fact that the four simulated architectures of fluctuation (Fig. 2A) are known *a priori*

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

203

204 **A simple demographic model in fluctuating environments**

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

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

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)

229 of a freshwater snail changed nonlinearly across the species' reproductive season. The exact shape
230 of vital rate response functions is another key point to be tailored for system-specific inquiry,
231 whether with empirical measurements or as realistic assumptions built into models.

232

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

234 For each of the four architectures of environmental fluctuations, we ask what the long-run fitness
235 of a life history would be. The modelled life history is defined as the set of vital rate parameters
236 $\{f, S_A, S_J\}$ in the demographic model, scaled for per time-step rates. We hold $f = 0.2$ and $S_A =$
237 0.95 constant to analyze the effect of fluctuations in S_J along its logistic function about its mean
238 = 0.5 (Fig. 3B). Note that these values are arbitrary but biologically realistic. For fitness, we use
239 the 'small-noise approximation' (Tuljapurkar 1982) of time-averaged fitness in variable
240 environments:

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

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

fluctuation noise affects the divergence of fitness estimates among the four architectures.

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 (Fig. 3C). 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 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 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.

(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,

291 here the juvenile survival rate S_J). This asymmetry is referred to as Jensen's Inequality (Jensen
292 1906; Ruel and Ayres 1999), which states that for a convex or concave function $f(x)$, the average
293 of the function, $\overline{f(x)}$, does not equal the function of the average, $f(\bar{x})$. Verbally, this means that
294 symmetrical fluctuation about the mean of a variable x along the x-axis does not translate
295 equivalently to symmetrical fluctuation about the mean along the y-axis. If we take fluctuation on
296 the x-axis as that of the environment, and fluctuation on the y-axis as that of demography, Jensen's
297 Inequality introduces a break in the environment-demography link in fluctuating environments
298 (Fig. 4B). The direction of that asymmetry (*i.e.,* $f(\bar{x}) \leq or \geq \overline{f(x)}$) as well as its magnitude
299 depend on the convex/cavity of the region of the nonlinear function where the mean lies. Here that
300 nonlinearly fluctuating variable is juvenile survival S_J, which has a direct effect on fitness $log\lambda_s$.

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

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

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

309 By manipulating the convex/cavity of the nonlinear demographic parameter S_J around the mean
310 (Fig. 5A), we explore further the biological consequences of the two interacting mathematical
311 mechanisms. When mean juvenile survival is low and its response function convex around the

312 mean (Fig. 5A, left panel), fitness increases with an increase in environmental variability (σ) due
313 to Jensen's Inequality (corresponding panel in Fig. 5B). Conversely, when mean juvenile survival
314 is high and its response function concave around the mean (Fig. 5A, right panel), fitness on average
315 is pulled down with an increase in environmental variability for the same reason (corresponding
316 panel in Fig. 5B). Across the convex/cavity spectrum of the logistic response function of juvenile
317 survival, as σ of the environmental fluctuation is increased from $0 \rightarrow 0.3$ ($0 \rightarrow 60$ time-steps,
318 since σ is proportional to mean interval = 200), the range of fitness estimates begins to converge
319 for all four environments ($log\lambda_s = 0.02{\sim}0.05$; Fig. 5B, note different y-axis ranges); this occurs
320 because with higher variance, fluctuations begin to sample from wider breadths of the logistic
321 response function which has a combination of convex and concave regions, rendering the role of
322 Jensen's Inequality weaker. Nevertheless, the relative ordering of fitness across environments (Fig.
323 5B, all panels) remains stable, demonstrating the interactive role that the consecutive deviation
324 patterns of environmental fluctuation architectures (mechanism 1) and the geometric nature of
325 $log\lambda_s$ play in differentiating fitness.

326

327 **Summary and Future Outlook**

328 Non-random fluctuations abound in nature, from temporally autocorrelated to externally driven
329 cycles (Sabo and Post 2008; Dunn and Møller 2014; Hacket-Pain and Bogdziewicz 2021), yet they
330 are less commonly treated in models and theory than pure stochasticity. We show that different
331 architectures of environmental fluctuations cause substantial and consistent divergence in
332 evolutionary fitness $log\lambda_s$, not just between random and non-random fluctuations, but also within
333 the non-random ones. Notably, these fitness differences arise from environmental sensitivity in

334 just one vital rate, juvenile survival, while adult survival and fecundity were modelled as
335 environment-independent. *A priori* knowledge or quantitative characterization of the nature of
336 fluctuations and how they affect vital rates can thus help us explain a greater breadth of population
337 dynamics and evolutionary trajectories of life histories across environments. Incorporating non-
338 randomness in environmental models is not new to many researchers working on life history theory
339 or demography. Developments in periodic matrix models (Caswell and Trevisan 1994), the
340 seasonal forcing of disease dynamics (Altizer et al. 2006), bet-hedging strategies (Venable 2007),
341 and the effect of temporal autocorrelation on life history evolution and population persistence (Pike
342 et al. 2004; Metcalf and Koons 2007; Tuljapurkar et al. 2009) are just a few of the examples. The
343 novelty of our results is two-fold: we show for the first time that a systematic comparison of
344 random and non-random (internally and externally driven) fluctuations reveals consistent
345 differences in fitness estimates of a life history; then, we demonstrate two simple mechanisms that
346 drive this divergence in fitness. These mechanisms are prevalent, and their treatment should open
347 new doors for investigating demography and selection dynamics in the diverse—and changing—
348 fluctuation architectures in nature.

349 Our results corroborate a message that has repeatedly emerged out of the theoretical literature of
350 colored noise and extinction risk, namely that "red" environments (positively autocorrelated)
351 increase extinction risk while "blue" environments (negatively autocorrelated) do the opposite
352 (Lawton 1988; Halley and Kunin 1999; van de Pol et al. 2011; Halley et al. 2018). Although we
353 focused on long-term fitness as opposed to extinction risk *per se,* the link to population persistence
354 is obvious: in positively autocorrelated environments, the long-run growth rate was not only lowest
355 by far, it also showed the highest amount of variance (Fig. 3C), increasing the likelihood of a
356 population crash proving fatal. In contrast, negatively autocorrelated fluctuations led to the highest,

357 most constant long-term fitness (Fig. 3C). Theory in this respect is somewhat incomplete, however,
358 as density-dependence and stage- or age-structure can create autocorrelation in population
359 dynamics themselves, making predictions challenging (Greenman and Benton 2003). Importantly,
360 we further distinguish autocorrelated environments from seasonal or otherwise fundamentally
361 cyclical ("Noisy Clock") ones, in that memory in the latter kind is anchored in physically
362 determined 'due' times, rather than in past environmental states. We show that long-term fitness
363 in Noisy Clock environments consistently falls in the middle of red and blue environments,
364 suggesting that modelling seasonal environments simply as autocorrelated with a dominant
365 frequency of 1 year might lead to erroneous conclusions. Mathematical proofs for this pattern
366 would be worthwhile for future work, particularly work concerned with forecasting population
367 growth and viability in Noisy Clock environments which are common in nature.

368 In reality, environmental fluctuations will seldom neatly fall into only one of the architectural
369 categories simulated here. For example, a coastal system that is strongly perturbed by periodic
370 tidal disturbances will also be controlled by a lower resonance of seasonal fluctuations (Denny et
371 al. 2009). How resonances of non-random fluctuations constructively or destructively interfere to
372 produce a variety of fluctuation superpositions in different ecosystems might explain a wider
373 breadth of observed life history diversity and population trajectories. Even if an environment is
374 predominantly driven by one type of fluctuation architecture, the similarity of the sample
375 distributions (Fig. 2) can make it difficult to unequivocally place a given environment into one
376 fluctuation category. Empiricists could consider plotting the distribution of consecutive deviations
377 relative to a long-term mean interval of events—or periodicity of fluctuation—as we did in Fig.
378 4A. The shape of this distribution, particularly compared against the null hypothesis of a stochastic
379 (purely random) distribution of consecutive deviations simulated with the measured long-term

380 mean and standard deviation, might give an indication of whether an environment is fluctuating
381 positively autoregressively (long tail), or negatively autoregressively / in a Noisy Clock fashion
382 (short tail). Climate scientists and population ecologists regularly use spectral analyses to detect
383 dominant periodicities and lag times in time series of disturbance events or continuous
384 environmental variables (Priestley 1981; Chatfield 2003; Sabo and Post 2008), though often to
385 remove temporal autocorrelation so long-term trends can be detected (Pyper and Peterman 1998;
386 Brown et al. 2011). We argue that consideration of such methods should become more common
387 for life history and evolutionary demography analyses in nature. Our demonstrations suggest that
388 interactions between the architecture of environmental fluctuation and nonlinear biological vital
389 rates (*e.g.* survival, growth, reproduction) will alter fitness estimates in a broad range of situations.

390 For generality, we strived to simplify our assumptions and structure of the modelling framework,
391 particularly with respect to life history complexity. We emphasize that these are likely fruitful
392 areas for expansion and customization for specific empirical tests. For instance, many species are
393 naturally structured into more than two stages, for example amphibians (*e.g.* egg, larva, adult) and
394 insects (*e.g.* egg, nymph, pupa, adult). The number and interconnectedness of life stages via growth,
395 survival, and reproduction might have other complex and interesting influences on how fitness
396 differs between fluctuation architectures. The nonlinear response function of a vital rate can take
397 many different shapes depending on the more proximate developmental, physiological, or
398 behavioral mechanisms, from quadratic to self-excitatory threshold to polynomial functions (Ellis
399 and Post 2004; Stenseth et al. 2004; Nevoux et al. 2008). However, regardless of the life history
400 complexity or functional response shape, the joint effect of the two mechanisms we elucidated
401 here (consecutive patterns in fluctuations and Jensen's Inequality) must be in play if there is any
402 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 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 based on widespread stochastic assumptions.

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Figures & Legends

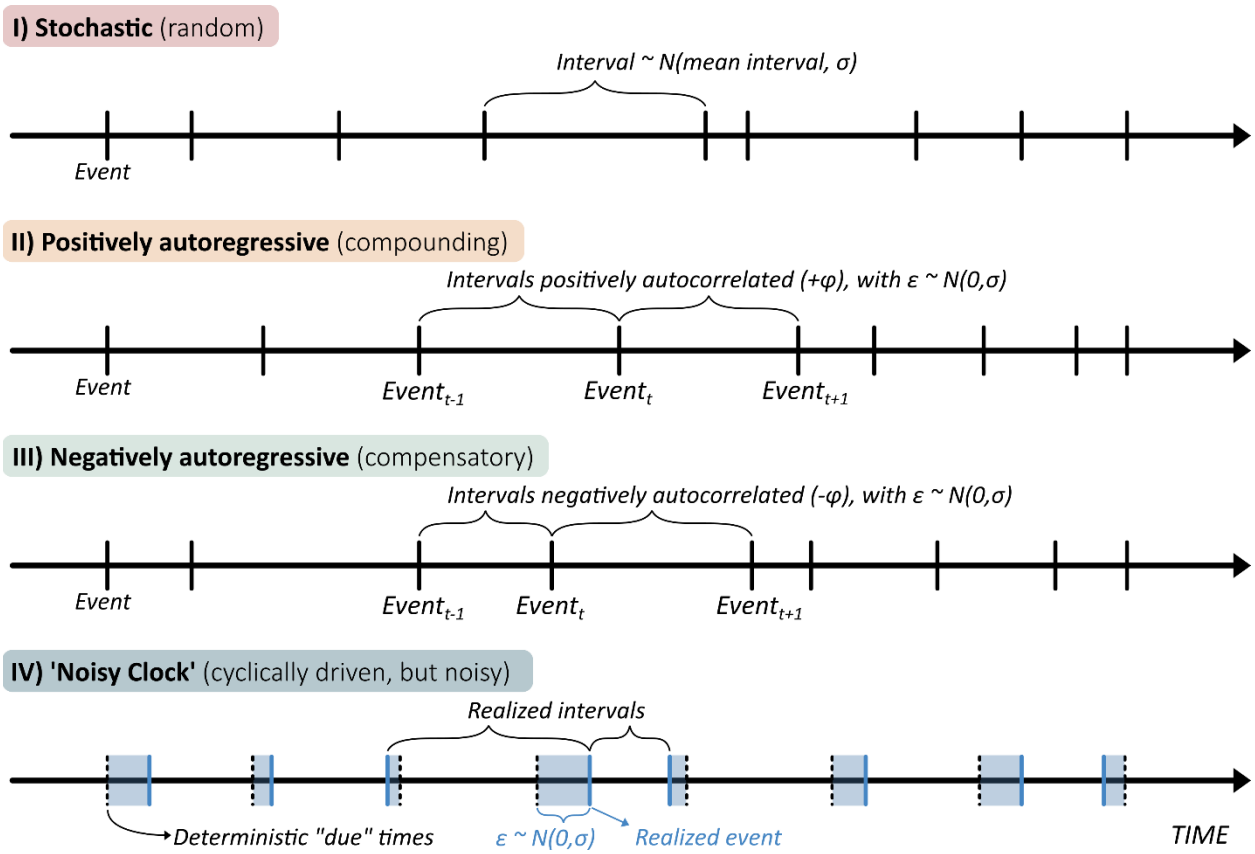


Figure 1. Four generating functions of fluctuating environments. Each fluctuation architecture is determined by the process of generating a sequence of discrete intervals between events on a continuous timeline.

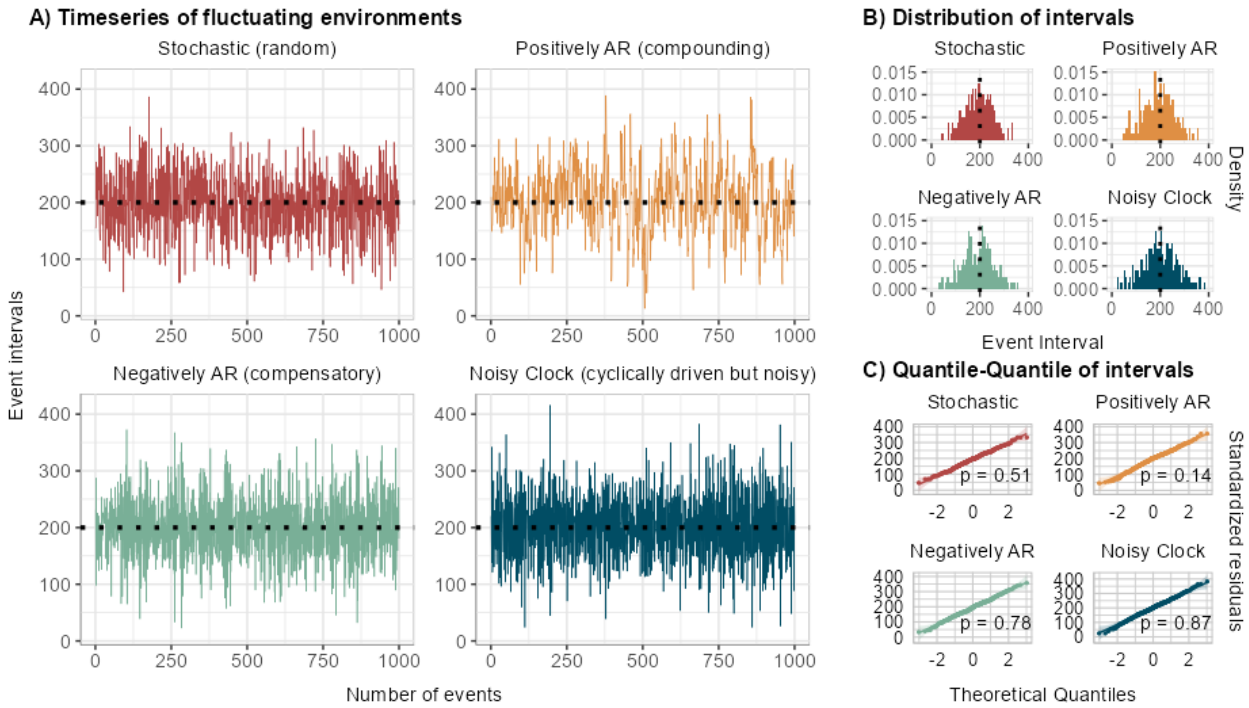
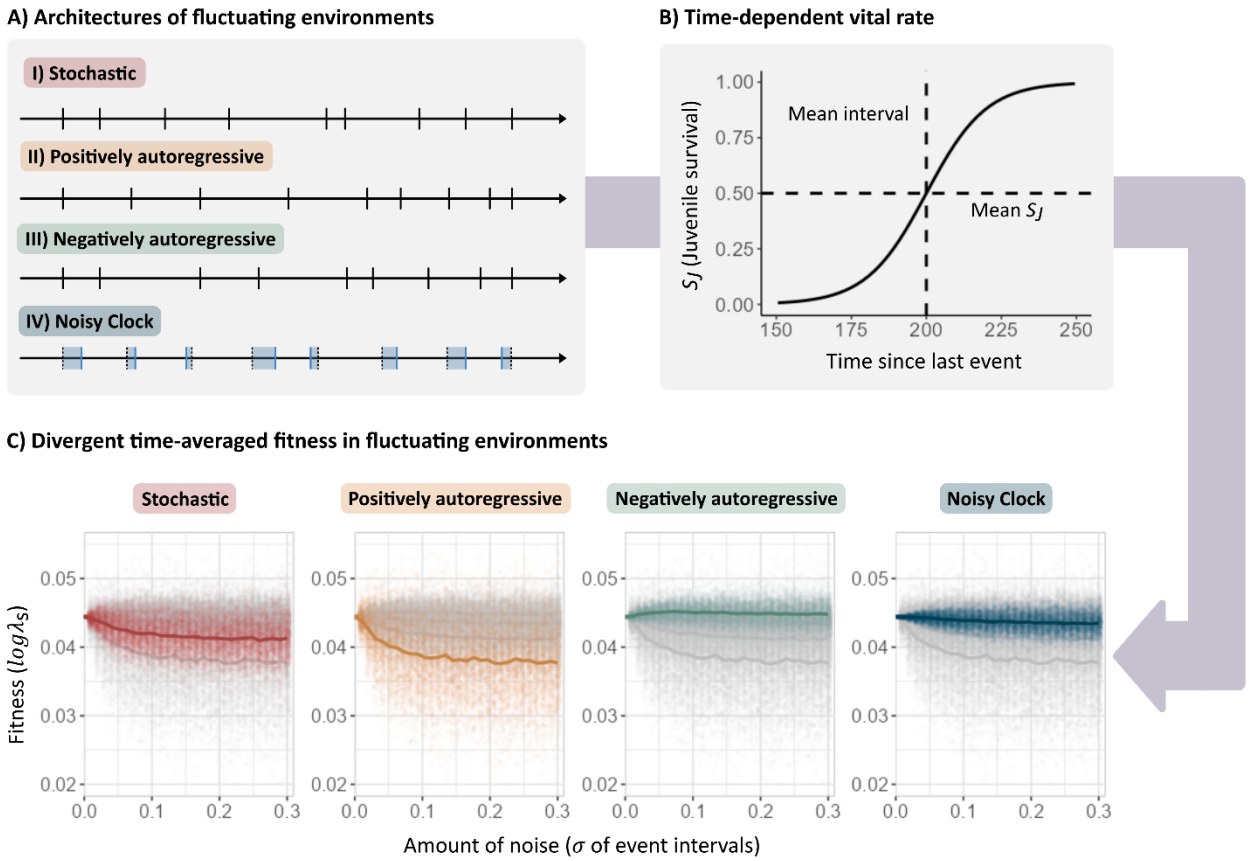


Figure 2. Visualizing the four generated environments. A) Time series of intervals over 1000 events are simulated with $\bar{X} = 200$ and $\sigma = 0.2 \times \bar{X}$. A multiplier of 1.3 was applied to the σ of the stochastic generating function to make the width of all four sample distributions more 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.



643

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

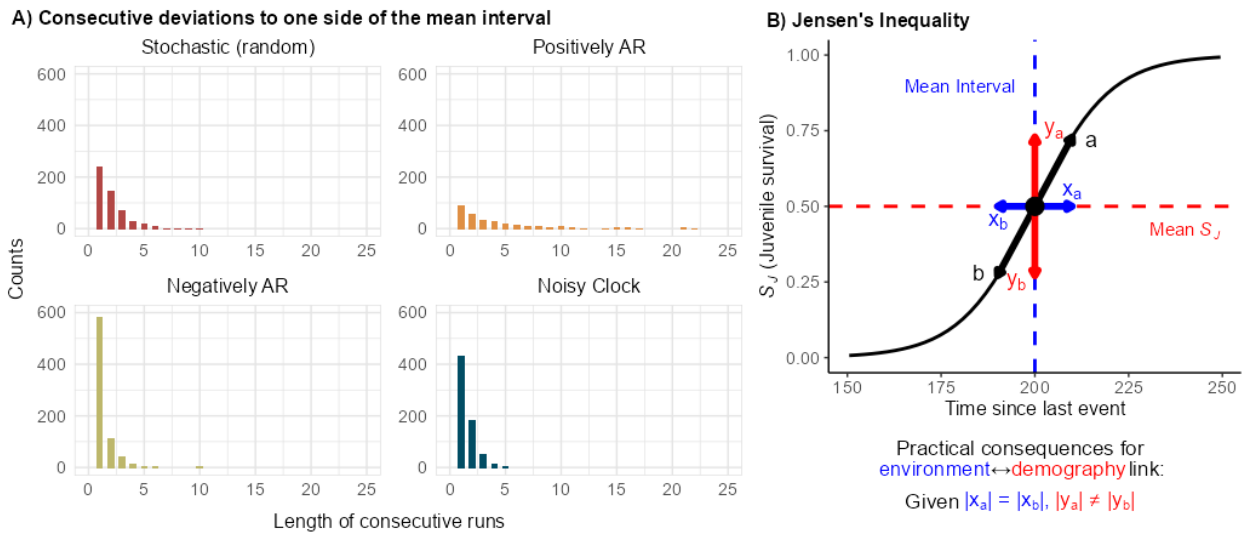
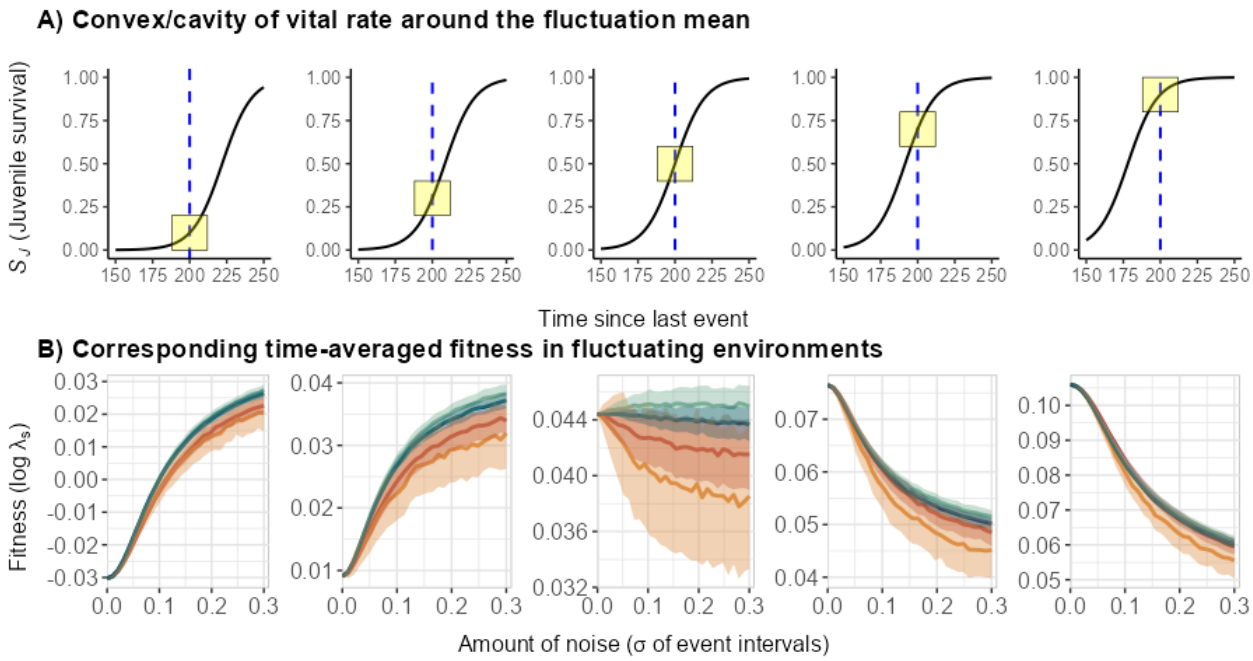


Figure 4. Mechanisms of fitness divergence between the architectures of fluctuating environments. A) Despite very similar long-term distributions of event intervals (Fig. 2), environments have very different distributions of consecutive runs to one side of (below or above) the mean interval depending 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.



669

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