The Importance of Noise Colour in Simulations of Evolutionary Systems

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Abstract Simulations of evolutionary dynamics often employ white noise as a model of stochastic environmental variation. Whilst white noise has the advantages of being simply generated and analytically tractable, empirical analyses demonstrate that most real environmental time series have power spectral densities consistent with pink or red noise, in which lower frequencies contribute proportionally greater amplitudes than higher frequencies. Simulated white noise environments may therefore fail to capture key components of real environmental time series, leading to erroneous results. To explore the effects of different noise colours on evolving populations, a simple evolutionary model of the interaction between life-history and the specialism-generalism axis was developed. Simulations were conducted using a range of noise colours as the environments to which agents adapted. Results demonstrate complex interactions between noise colour, reproductive rate, and the degree of evolved generalism; importantly, contradictory conclusions arise from simulations using white as opposed to red noise, suggesting that noise colour plays a fundamental role in generating adaptive responses. These results are discussed in the context of previous research on evolutionary responses to fluctuating environments, and it is suggested that Artificial Life as a field should embrace a wider spectrum of coloured noise models to ensure that results are truly representative of environmental and evolutionary dynamics.

Keywords
Coloured noise, evolutionary dynamics, life-history evolution, variable environments, fluctuating environments, evolved generalism

1 Introduction

Numerous modelling and simulation approaches in artificial life, biology, ecology, and other disciplines require initial input of a stochastic environmental time series to which agents or individuals respond. Frequently the time series used represent white noise, as this is easily simulated and generally regarded as a simple and useful way to introduce an environment that varies randomly. Minimally, a *white noise time series* is defined as one without significant autocorrelation at any lag other than zero. In practice, white noise is often created from a series of independent, identically distributed random variables with zero mean and finite variance, with the generating distribution

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often Gaussian. Due to the lack of autocorrelation, the power spectral density of white noise is flat, with equal power in any given frequency band. It is this latter characteristic that gives white noise its name, by analogy with the approximately flat power spectral density of white light over the visible range.

Though there are many instances in which white noise is a valuable approximation of a fluctuating environment—its stationarity, lack of memory (≈ autocorrelation), and long-term symmetry are valuable properties that facilitate analysis—it is not realistic as a depiction of real environmental fluctuation in the majority of cases. Empirically, most environmental and ecological time series fall within the pink to red noise spectrum, in the sense that their power spectral densities display greater power at lower frequencies. Empirical records of marine and terrestrial temperatures, precipitation and river levels, and ecological phenomena such as population fluctuations, persistence times, and times to extinction are all found to exhibit power spectral densities with these "reddened" properties (Cuddington and Yodzis, 1999; Halley & Inchausti, 2004; Inchausti & Halley, 2001, 2002; Mandelbrot & Wallis, 1969; Miramontes & Rohani, 1998; Steele, 1985; Vasseur & Yodzis, 2004). As an example, Figure 1(a) shows the terminal Pleistocene section of the North Greenland Ice Core Project (NGRIP) benthic $\delta^{18}O$ data (Rasmussen et al., 2014)—an isotopic ratio proxy for temperature—with Figure 1(b) showing the power spectral density of these data.

The exponent (β) marked on Figure 1(b) is the (negative) slope of the black line, and is used to measure the *colour* of the time series. The equation relating power (p) to frequency (f) is then:

$$\text{In}\ (p) \propto 1/\ln(f)^{\beta} \tag{1}$$

This format leads to the closely related concept of $1/f$ noise frequently encountered in the physical sciences literature. In the format of Equation 1, $\beta = 0$ equates to white noise, $\beta = 1$ to pink noise, and $\beta = 2$ to red noise. Perfect pink noise at $\beta = 1$ is a special case in that power is the exact reciprocal of frequency, but in practice the definition of pink noise is often extended to refer to a wider region around this particular case with $0.5 \lesssim \beta \lesssim 1.5$. The NGRIP benthic $\delta^{18}O$ data display a power spectral density in the pink to red spectrum, as is common with empirical palaeoclimatic and palaeoenvironmental time series.

Figure 2 shows examples of simulated white, pink, and red time series together with their associated power spectral density plots. In relation to empirical data it is important to note that time series in the pink to red range—those with greater power at lower frequencies—allow for longer-term excursions of the time series that result from increased autocorrelation. At millennial and longer timescales, empirical palaeoclimatic signals are heavily influenced by long-term oscillations such as those resulting from the Milankovitch cycles that affect the amount of solar radiation reaching the earth and govern the transitions from glacial to interglacial periods. Though not all empirical records are perfectly characterized by the linear approximation of Equation 1, the coloured noise framework

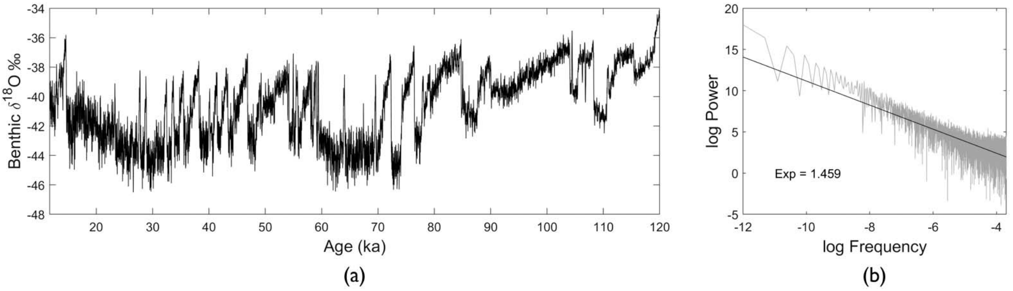


Figure 1. The Late Pleistocene section of the benthic $\delta^{18}O$ record from the North Greenland Ice Core Project (NGRIP). (a) shows the time series itself, and (b) its logarithmically transformed power spectral density. The black line fitted to the data in (b) represents the equation $\ln(p) = 1/\ln(f)^{1.459}$, indicating that the time series has a power spectral density between pink and red noise.

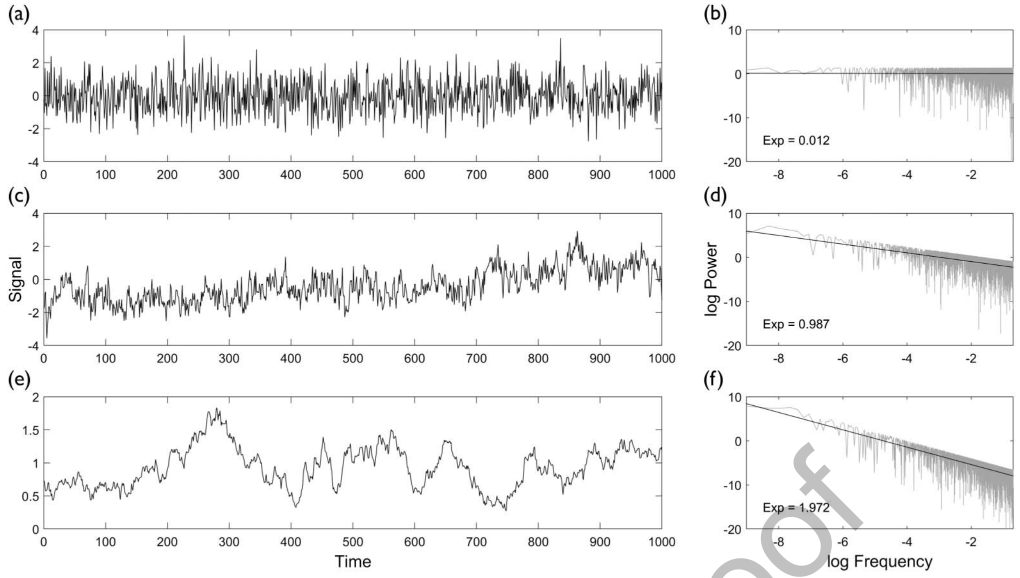


Figure 2. Examples of simulated white (a), pink (c), and red (e) time series. Respective power spectral densities are shown (logarithmically transformed) in (b), (d), and (f). The black lines fitted to the data in these latter three plots represent equations of the form $\ln(p) = 1/\ln(f)^{\beta}$. Exact values of β are given in the plots, and closely resemble white ($\beta = 0$), pink ($\beta = 1$), and red ($\beta = 2$) noise.

remains a valuable shorthand for describing time series, and importantly includes white noise as a special case.

Stochastic simulation models are highly important in many disciplines, and are a necessity when dealing with responses to natural environments, which are highly variable through time and often unpredictable. As there are many sources of environmental variability, and as these combine additively to create the fluctuations observed empirically, white noise (particularly Gaussian white noise) seems at first to be a logical choice as a proxy environment. However, different sources of variation act at different frequencies and provide contributions of differing amplitude to the overall pattern of environmental fluctuation; empirical studies suggest that in general lower-frequency sources of variation are of higher amplitude than higher-frequency sources of variation, and this finding suggests that time series with pink to red power spectral densities may be more realistic as proxies for real environments.

The fact that empirical environmental and ecological time series rarely conform to white noise suggests that models could be made more realistic by extending them to encompass other colours of noise. Critically, it is important to assess whether models of evolutionary processes that employ white noise produce results that differ from those employing more realistic pink or red noises (Grove et al., 2020). Using a simple model of the trade-off between specialism and generalism, Grove and colleagues demonstrate that markedly different results are generated when time series of different colours are used as the environments to which agents adapt. Below, we report this model, which we then extended to include differences in the reproductive rate of the species modelled in order to study the interactions of noise colour, reproductive rate, and the specialism-generalism trade-off. Reproductive rate (or life history more generally) is a fundamental part of a species' adaptation; despite a growing interest in coloured noise environments among ecologists and environmental scientists in recent years, however, the interaction of noise colour and life history remains a largely neglected area of research.

1.1 Coloured Noise Research in Ecology and Evolution

Coloured noise research within ecology in recent years has seen a focus on evolutionary changes in population size, and particularly on the effects of noise colour on extinction risk. Ripa and Lundberg (1996) applied the Ricker model of population growth (Ricker, 1954) to show that redder noise lessens the risk of extinction, concluding that autocorrelation was critical in determining whether a population grew (under red noise) or declined, ultimately to extinction (under blue noise, with $\beta < 0$). Similar results were obtained by Cuddington and Yodzis (1999), using another variant of the Ricker model that explicitly included coloured noise (see also Petchey et al., 1997), extending the noise colours to encompass black noise with $\beta \to 3$. Extremely high values were found to be associated with increasingly long population persistence times compared to less reddened noise $(0.5 \leq \beta \leq 1)$, suggesting that evolution under highly autocorrelated noise produces robust populations that can adapt effectively to rare but potentially highly significant environmental events. The conclusions of Cuddington and Yodzis (1999) are confirmed by Halley and Kunin (1999) and Inchausti and Halley (2001, 2002, 2003), all of whom note that the effect of reddening is to increase the variance observed in longer time series but that, contrary to the expectation that populations are more likely to become extinct in more extreme environments, evolution in such conditions is more robust to environmental variance. Cuddington and Yodzis (1999) also note that white noise, with its lack of autocorrelation, does not capture the features of the natural environments within which evolution occurs. These simulations demonstrate that different frequencies of coloured noise profoundly affect population dynamics, and that research must extend beyond traditional white noise models to establish realistic simulations of environmental fluctuation.

Halley (1996) proposes pink noise as the most suitable model of a typical environmental time series. His proposal rests on the fact that white noise, consisting of equal power at all frequencies and lacking any form of autocorrelation, under-represents rare but significant disruptive events, whereas red noise over-emphasises longer-term periodicities. Pink noise, however, gives equal weight to both common and rare environmental events. Further to this, Inchausti and Halley (2002) demonstrate that animal population dynamics display pink noise far more often than would be expected given the power spectral densities of the environmental time series that the populations are exposed to. Halley and colleagues suggest that time series towards the reddened end of spectrum, rather than white noise, produce ecologically valid models of environmental variability; pink noise, with its proportional power across the frequency range, its long memory, and its non-stationarity, shows important characteristics present in empirical ecological time series (Halley & Inchausti, 2004).

Evolution responds to environmental variability over multiple timescales by mitigating the risk associated with both short-term and long-term environment change, maximising immediate fitness whilst also ensuring continued survival. Under real environmental fluctuations, evolution can select for individuals who are generalists rather than specialists, favouring plasticity to increase the long-term likelihood of population endurance (Haaland et al., 2019, 2020). To explore how different colours of noise affect the trade-off between specialism and generalism in fluctuating environments, Grove (2014) and Grove et al. (2020) developed a simple evolutionary model of this trade-off. They confirmed that generalism was more likely to evolve as environmental variability became whiter, whilst specialism was more likely to develop under redder environmental variability; importantly, pink noise was found to be the point of balance between selective regimes favouring generalism and specialism. However, Grove et al. (2020) note that since recombination events (a major generator of genotypic variation in sexually reproducing species) occur with less frequency in organisms with longer generation times, there is potentially a confounding relationship between life history and the development of environmental tolerance in populations experiencing different colours of environmental noise.

1.2 Evolution in Fluctuating Environments

There is a substantial body of research in evolutionary biology examining the relationships between fluctuating environments and generalism, plasticity, niche breadth, and environmental tolerance (Baker, 1965; Grove, 2015; Levins, 1968; Mayr, 1965; Moran, 1992; Sol, 2008). Some of these terms are used interchangeably in the literature; although there are subtle differences, conclusions can be generalised by stating that most previous research suggests that increases in temporal environmental heterogeneity produce more eurytopic organisms. Eurytopic organisms are able to tolerate a wide range of habitats and environmental conditions; this can be achieved via generalism or plasticity, and necessitates increases in niche breadth and environmental tolerance.

An extensive series of analyses, beginning with initial genetic research by Levene, Dempster, and others (Cohen, 1966; Dempster, 1955; Gillespie, 1973; Haldane & Jayakar, 1963; Levene, 1953; Lewontin & Cohen, 1969) has suggested that temporal heterogeneity in environmental conditions is likely to promote the evolution of various forms of flexibility or plasticity at the individual or population levels. Much early research focussed on the maintenance of genetic polymorphisms via mechanisms such as heterozygote advantage, but such research also provided a basic mathematical template for the study of evolutionary dynamics in fluctuating environments across far broader scales (Lee & Doughty, 2003; Simons, 2002). In essence, the contrast between selection in spatially and temporally heterogeneous environments rests on the distinction between the arithmetic and geometric means. An organism that encounters differing environmental states across space ($\approx$ simultaneously) will have an overall fitness that is the arithmetic mean of its fitnesses in those states. If these environmental states differ only spatially, with each being constant through time, the arithmetic mean will be identical in each generation for organisms utilising the same territory; there will therefore be no variance in fitness between generations. If environmental states change through time, however, such that subsequent generations experience different environmental mosaics, the appropriate measure of fitness becomes multiplicative, and the *geometric mean effect* comes into play (Carja et al., 2013; Lee & Doughty, 2003; Simons, 2002).

The geometric mean is highly sensitive to variance, and therefore the most successful lineages of organisms in the long-term will be those that minimise variance in fitness between generations rather than maximising (arithmetic) mean fitness within generations. Eurytopic organisms naturally fulfil this criterion, whether via generalism or plasticity; they may never be the fittest organisms in a particular environment, but they are also rarely the least fit organisms in that environment. Dobzhansky's (1950, p. 216) observation that temporally variable environments "put the highest premium on versatility rather than on perfection in adaptation" remains one of the clearest statements of this principle. A series of more recent studies have explicitly examined fluctuations in autocorrelated environments, with a particular focus on the evolution of bet-hedging strategies (e.g., Carja & Creanza, 2019; Libby & Ratcliff, 2019; Wang & Dai, 2019). Wang and Dai (2019) suggest that generalist phenotypes evolve under intermediate levels of environmental correlation, while Libby and Ratcliff (2019) argue that structured populations and dispersal can maintain sufficient genetic variance at the population scale to reduce the risk of extinction in unpredictable environments. Carja and colleagues (e.g., Carja & Creanza, 2019) extend such approaches to examine "cultural bet-hedging" (see also Grove, 2018, 2019) and the evolution of diversity in populations of socially learning organisms.

It is important to note, however, that the relationship between autocorrelation and noise colour is neither linear nor simple. The equation for iteratively generating an autocorrelated time series is frequently given as

$$\phi_{t+1} = \alpha\phi_t + \epsilon_{(t+1)} \tag{2}$$

where ϕ is the time series, α is the autocorrelation parameter, and ϵ is a series of normally distributed random variates with zero mean and unit variance. It is then often assumed that the autocorrelation parameter α relates to the β parameter in $1/f^{\beta}$ noise (at least in the region between white [$\beta = 0$] and red [$\beta = 2$] noise) as $\alpha = \beta/2$. However, there exists no simple linear relation of this kind between autocorrelated and $1/f$ noise, as shown via simulation in Figure 3. Figure 3 shows the β value realised when simulating autocorrelated environments according to Equation 2; beyond white noise, for which $\alpha = \beta = 0$, the simulation results deviate considerably from the assumed relationship of $\alpha = \beta/2$. This deviation is caused by the fact that Equation 2 describes an

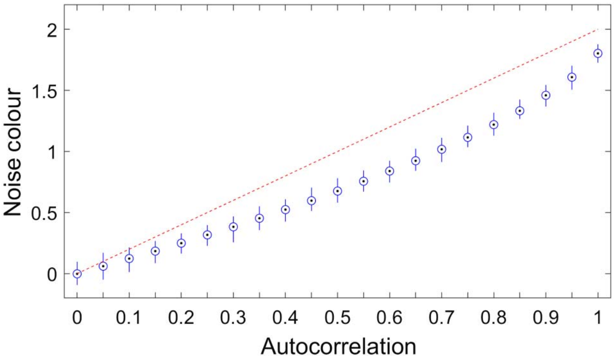


Figure 3. The relationship between the autocorrelation parameter of Equation 2 and the noise colour of the resultant time series. Each data point represents the median noise colour of 1,000 time series generated via Equation 2; whiskers represent the full range of variation around the median. The red dashed line represents $\beta = 2\alpha$ where β is the exponent of a coloured noise series $1/f^{\beta}$ and α is the autocorrelation parameter of Equation 2.

AR-1 process whereas coloured noise consists of self-similar patterns of recurrence across the entire time series.

1.3 The Interaction of Life History and Environmental Fluctuation

Animals have been found to show substantial variation in life history variables, as characterised in Pianka's (1970) expansion of MacArthur and Wilson's (1967) *Theory of Island Biogeography*. Pianka's (1970, p. 593) focus on *r*- and *K*-selected species differentiates between organisms of small body and brain size, which develop rapidly, reach sexual maturity early, and have short lifespans (*r*-selected species), and those of large body and brain size, which develop slowly, take longer to reach sexual maturity, and show greater longevity (*K*-selected species). Though these conditions are necessarily relative rather than absolute, and the theory has received considerable criticism (reviewed in Reznick et al., 2002), the basic essence of the theory—that animals can be organised on a life history continuum between those that have "fast" reproductive rates (*r*) and those that have "slow" reproductive rates (*K*)—is evidently true, and continues to permeate the literature (e.g., Engen & Sæther, 2017; Lande et al., 2017; Wright et al., 2019). Importantly, Bromham (2009, 2011) notes that if reproductive rates vary between species, then rates of potential evolution must also vary. This is due to the fact that mutation rates vary considerably between species (e.g., Bromham et al., 1996; Lanfear et al., 2010), with a substantial part of this variation correlated with life history variables such as reproductive rate (e.g., Nabholz et al., 2008; Nikolaev et al., 2007). Since mutation provides the raw material for evolutionary change, the potential for evolutionary change is greater in those species with higher reproductive rates. This leads to the theory that rapidly reproducing species may be more able to track environmental fluctuations via natural selection, whereas slowly reproducing species may be more dependent upon behavioural adaptation, individual and social learning, and, ultimately, cultural evolution (e.g., Grove, 2017, in press).

Modifications and extensions of Pianka's (1970) classification are too numerous to cover in detail, but of relevance to the analyses below is the finding of Bielby and colleagues (Bielby et al., 2007) that there may not be a single axis of variation corresponding to the continuum between fast and slow species. Whilst Stearns (1983) argued for the existence of both fast-slow and precocial-altricial life history axes, factor analyses conducted by Bielby et al. (2007) suggest that, after controlling for body size, the two main factors concern the timing of reproductive bouts and the reproductive output per bout. Age at sexual maturity, inter-birth interval, and weaning age load heavily on the first factor, with gestation length and litter size associated with the second factor. Modelling efforts may ultimately have to incorporate these two factors separately, but overall measures of reproductive output such as the maximum intrinsic rate of increase ($r_{\max}$) remain useful as summaries of a species' position on the classic life history continuum between fast and slow.

The response of a species to environmental change has been found to be strongly affected by life history. Chiba (1998) predicts that, under gradual climatic change, *K*-selected species inhabiting previously stable environments would face the most serious risk of extinction, whilst modelling by Benton & Grant (1996) and Tuljapurkar (1989, 1990) suggest that *r*-selected organisms would be most severely impacted by rapid climate perturbation and catastrophic events. These outcomes may seem contradictory, yet they make sense in terms of life history theory. *K*-selected species, characterised by great competitive capability and high chance of survival to adulthood but low reproductive yield, are anticipated to persist in stable environments (MacArthur & Wilson, 1967). Such animals with slow life histories are found to be resistant to environmental disruption but lack the ability to rebound from long-term change due to their low reproductive rate. On the other hand, *r*-selected species have a higher capacity for reproduction and therefore tend to occupy more varied environments in the short term, avoiding extinction by recolonisation and tracking environmental change (Pribil & Houlahan, 2003). Behavioural and/or genetic adaptions allow animals with faster generation times to react quickly to climate change, improving their likelihood of survival. This together suggests that there are likely to be complex evolutionary responses to environmental change; crucially, species with differing life histories may respond in quite different ways to different types of environmental change. Based on previous work, both slower life histories and "whiter" environments are predicted to produce increased selection for generalism as opposed to specialism, but there has to date been no research into the interaction of these two effects.

To examine the interaction of noise colour and life history, the model described below extends the work of Grove and colleagues (Grove, 2014; Grove et al., 2020) by varying the reproductive rates of the simulated populations. Specifically, the model assumes a constant overall population size while varying *R*, the proportion of individuals replaced each iteration. Modelling life history in this way does not vary $r_{\max}$ (as the number of births is equal to the number of deaths in each iteration of each simulation, which is equivalent to assuming a constant carrying capacity); instead, increasing the replacement proportion mimics the effects of a faster life history in that it increases the amount of genetic variation produced via recombination in each iteration. The replacement proportion also acts as a viable proxy for both generation time and longevity, as both are directly related to its reciprocal; both the average longevity of an agent (in units of iterations) and the average number of iterations required to completely replace the existing population are equal to $1/R$.

1.4 Environmental Variability in Artificial Evolutionary Systems

Artificial evolutionary systems, often employed in artificial life, evolutionary robotics, computational biology, and computational social sciences, employ a variety of methods to either inject noise into the environment, or to vary the environment over time. Examples include the addition of noise to external forces (Bongard & Pfeifer, 2003) or sensor inputs (Jakobi, 1997; Jakobi et al., 1995) in evolutionary robotics; the application of an external environment (i.e., time-dependent changing of objective functions) (Borg & Channon, 2012; Bullinaria, 2018; Grove, 2014, 2018); the time-dependent determination of rewards/punishments (Canino-Koning et al., 2016); the varying of task difficulty over time (either predetermined, or determined by the performance of agents) (Borg et al., 2011; Jolley et al., 2016; Stanton, 2018; Stanton & Channon, 2013); and the exploration of complex and noisy environments for the emergence of open-ended evolution (Channon, 2019; Channon & Damper, 1998). In all of these examples, one thing is consistent—agents are expected to adapt to changes or uncertainty in their environment. The approaches taken to implementing this change or uncertainty vary significantly between systems. These implementations include the application of coloured noise, typically white noise/Gaussian random noise (Jakobi, 1997; Jakobi et al., 1995; Kouvaris et al., 2017) or, to a lesser extent, red noise/Brownian noise (Steiner, 2012; Whitehead & Richerson, 2009). Other implementations include the use of sine waves to determine environmental fluctuations over time, or variations on this theme (Borg & Channon, 2012; Grove, 2014, 2018; Khan et al., 2020; Stanton, 2018; Stanton & Channon, 2013). A final common approach is to predetermine a series of states which an environment could be in, and move between these states given a certain frequency, this frequency determining the difficulty or harshness of environmental change (Asakura et al., 2015; Canino-Koning et al., 2016; Ellefsen, 2014; Nolfi & Parisi, 1996; Ofria & Lalejini, 2016; Wilder & Stanley, 2015). One thing is common across all of these approaches, they all rarely consider pink noise, or ground the method of environmental uncertainty in empirical observations.

The application of environmental variability or noise is used to address a number of questions concerned with the affects of environmental uncertainty. The most common amongst these are whether changing environments affect: the emergence of phenotypic plasticity (Kouvaris et al., 2017; Wilder & Stanley, 2015) and evolvability (Canino-Koning et al., 2016; Ofria & Lalejini, 2016; Steiner, 2012); the evolution of robust controllers in 3D virtual creatures (Stanton, 2018; Stanton & Channon, 2013) and robots (physical and simulated) (Asakura et al., 2015; Bongard & Pfeifer, 2003; Jakobi, 1997; Jakobi et al., 1995); and the evolution of versatile adaptations such as learning (Ellefsen, 2014; Nolfi & Parisi, 1996) and social learning (Borg & Channon, 2012; Bullinaria, 2018). What is common amongst all these questions and domains is that they are seeking to understand the interaction between changing environments, specialist-generalist evolutionary dynamics, and adaptability. The work of Grove (2014) provides a suitable general framework for addressing the question of specialist-generalist evolutionary dynamics under environmental variability in artificial evolutionary systems, with Grove et al. (2020) demonstrating the benefits of accommodating coloured noise under this framework, and the importance of considering coloured noise as the basis for environmental variability and uncertainty as opposed to the more common methods discussed above.

2 Methodology

The model is based on a population of 1,000 agents each possessing a chromosome consisting of just two loci. These loci are continuous variables corresponding to the mean (Locus 1) and standard deviation (Locus 2) of a Gaussian distribution that describes an agent's environmental tolerance. Locus 1 therefore represents the environment in which the agent achieves its optimal fitness and can take any value, while Locus 2 represents how sharply the agent's fitness declines when the environment differs from this optimum and is necessarily positive. Agents with relatively low values at Locus 2 can be considered specialists, whereas those with relatively high values at Locus 2 can be considered generalists. Locus 2 can also therefore be considered a measure of an agent's niche breadth in a single dimension. At the start of each simulation, agents are initiated with Locus 1 values randomly distributed as $\mathrm{N}(0, 0.1)$ and Locus 2 values as $|\mathrm{N}(0, 0.1)|$ with $\mathrm{N}(\mu, \sigma)$ a Gaussian random variable. During each iteration of a simulation, each agent is assigned a fitness score calculated via a standard Gaussian function, given as:

$$F\left(a_{i,t}\right) = \frac{1}{\sigma_{i,t}\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{E_t - \mu_{i,t}}{\sigma_{i,t}}\right)^2} \tag{3}$$

where $F(a_{i,t})$ denotes the fitness of agent i at time t, E_t denotes the environmental value at time t, and $\mu_{i,t}$ and $\sigma_{i,t}$ denote respectively the values at Locus 1 and Locus 2 of agent i at time t.

Each iteration R individuals are chosen for reproduction via *fitness-proportionate selection* (henceforth FPS); a mutated copy of each of these individuals is produced, with these copies taking the place of the least fit R individuals in the population. Reproduction is therefore asexual, with the two loci fully linked; alternative simulations utilising sexual reproduction with values at the two loci inherited separately from two parents chosen independently via FPS did not appreciably alter the results. The mutation equations differ slightly for the two loci due to the necessity for positive values at Locus 2. Mutation at Locus 1 is given by:

$$L_1' = L_1 + \mathrm{N}(0, 0.1) \tag{4}$$

and mutation at Locus 2 by:

$$L_2' = L_2 \cdot e^{\mathrm{N}(0,0.1)} \tag{5}$$

where the prime indicates the mutated value at the respective locus in the new agent. The coloured noise time series to which agents adapt are generated via the inverse fast Fourier transform (henceforth IFFT), which allows for accurate generation of coloured noise. Time series were generated from a vector of frequencies $f = t/2s/n$, with $t = (s, 2s, \ldots, ns)$, a vector of sampling times, s the sampling period, and n a scalar equal to the length of the vector t. The sampling frequency is therefore $1/s$ with the Nyquist frequency equal to $1/2s$. The vector of desired amplitudes at each frequency is then calculated as:

$$A = \sqrt{\frac{1}{2}|1/f^{\beta}|} \tag{6}$$

where β is the log-spectral exponent (e.g., $\beta = 0$ for white noise, $\beta = 2$ for red noise). A is then doubled in length from n to $2n$ by adding an inverted copy to the bottom of the existing vector. A is then multiplied by an exponentiated vector of $2n$ random phase angles and passed to the IFFT, with the final coloured noise series calculated as:

$$E_{\beta} = R\left(IFFT\left\{A \circ \left(e^{2\pi u\sqrt{-1}}\right)\right\}\right) \tag{7}$$

where u is a vector of $2n$ uniformly distributed random numbers on the interval $[0, 1]$, $\circ$ indicates the Hadamard product (element-wise multiplication), and R indicates that only the real part of the complex output is retained. The vector E_{β} is now a coloured noise time series of length $2n$ with log-spectral exponent β. Time series were scaled to have zero mean and unit variance before being incorporated into the model. Two sets of tests were undertaken, the first with R fixed to replace half of the population (also reported in Grove et al., 2020), and a second set of tests where R is varied. For simplicity and to reduce padding during the IFFT procedure, $s = 1$ in all tests. In the first set of tests $n = 2^{16} = 65{,}536$, and in the second set of tests $n = 2^{12} = 4{,}096$; this leads to coloured noise series consisting of $2n = 131{,}072$ and $2n = 8{,}192$ timesteps respectively. The reason for reducing the length of the coloured noise series in the second set of tests was that it was clear from the first set of tests that simulations had stabilised early into the test and therefore did not require time series of such length. To examine the interaction of noise colour and reproductive rate, simulations were run on time series with log-spectral exponents from 0 to 2 in increments of 0.1 and reproductive numbers R from 50 to 950 in increments of 50 (corresponding to a range of 5% to 95% of the population replaced each iteration), yielding a total of 399 simulation runs. Population medians and 2.5th and 97.5th percentiles were recorded for Loci 1 and 2 each iteration. To produce a measure of central tendency indicative of a whole simulation run, the median of all agents across the last 130,000 (in the first set of tests) and 8,000 (in the second set of tests) iterations was calculated for both loci; to produce a measure of dispersion (population diversity) indicative of a whole simulation run, the median distance across the last 130,000 or 8,000 iterations between the 2.5th and 97.5th percentiles of the population was calculated for both loci.

3 Results

As first reported in Grove et al. (2020), our first set of simulations found that agents are more successful at tracking environments under reddened noise (increased values of β), as shown in the 2,000-iteration snapshots of example runs in Figure 4. Conversely, greater tolerance is selected for under whiter noise ($\beta \to 0$) as agents are unable to closely track the environment. This pattern is demonstrated by Figure 5 (top). We found that greater tolerance implies lower fitness (Figure 5,

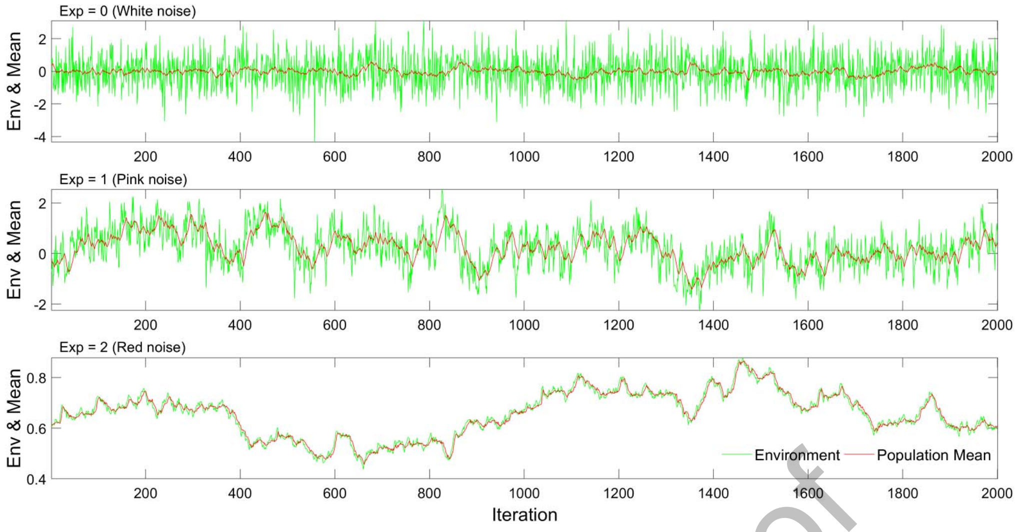


Figure 4. Three 2,000-iteration snapshots of single model runs where the proportion of agents replaced each iteration = 0.5. Agents are better able to track reddened noise, whereas the trajectory for white noise suggests that agents evolve towards the running mean of the environmental series and couple this with a broader environmental tolerance.

bottom) as agents are required to generalise to fluctuating environmental conditions rather than specialise under relatively stable redder noise. Evolution under pink noise, however, provides an intermediary between white and red noise. To understand the relationship between noise colour and the rate of change in evolved tolerance, we applied a local polynomial regression method, known as

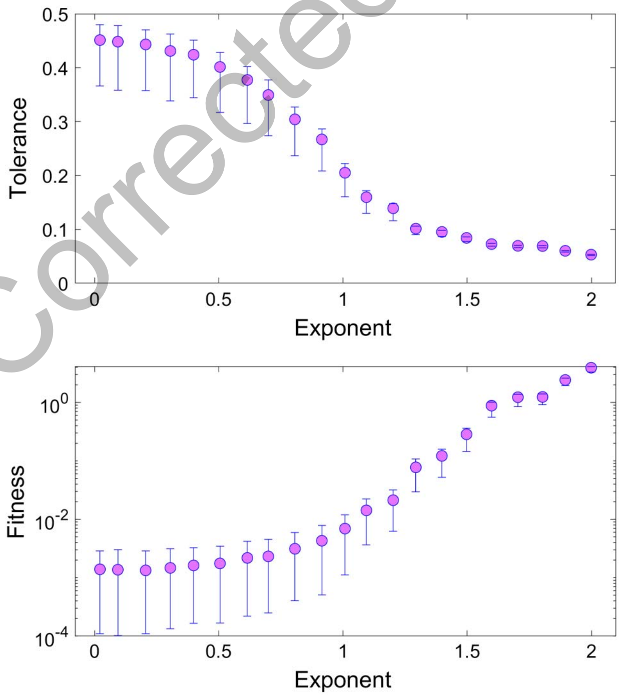


Figure 5. Tolerance and fitness values for populations evolving in environments characterised as white $1/f^0$ to red $1/f^2$ noise, where the proportion of agents replaced each iteration = 0.5. In line with the snapshots of Figure 4, whiter noises require greater levels of tolerance and result in accordingly lower fitness. Points show medians, and error bars show 2.5th and 97.5th percentiles, each over the last 130,000 iterations of a given run.

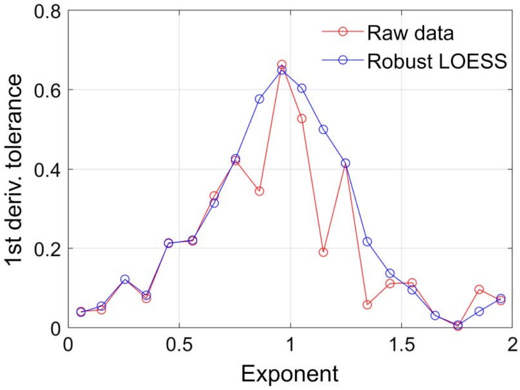
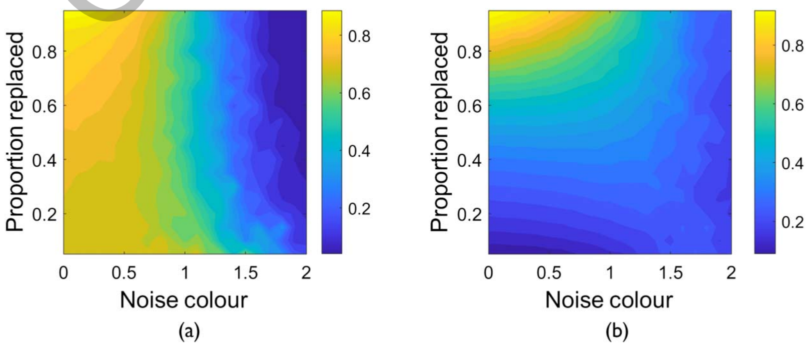


Figure 6. A robust LOESS curve fitted against the first derivative of raw tolerance data where the proportion of agents replaced each iteration = 0.5 (as seen in Figure 5). The fitted curve demonstrates that the rate of change in tolerance against the noise exponent peaks at pink 1/*f* noise.

robust locally estimated scatterplot smoothing (LOESS), to the first derivative of the raw tolerance data (see Figure 6). This shows that pink noise is the central point of the exponent, with the shift from white to pink eliciting a rate of change in evolved tolerance that increases to its peak, which falls away as the environment reddens beyond pink noise. Pink noise is thus the pivot between two relatively stable evolutionary states: high tolerance in white noise environments and low tolerance in red noise environments.

Similarly, in our second set of simulations, environmental tolerance values (as represented by Locus 2) decreased as the environmental noise became increasingly reddened. However, a more nuanced pattern is returned when considering the interaction between different noise colours and reproductive rate. As shown in Figure 7(a), populations experiencing relatively white noise ($\beta \rightarrow 0$) evolved greater environmental tolerance under higher reproductive rates, whereas populations experiencing relatively red noise ($\beta \rightarrow 2$) evolved lower environmental tolerance under higher reproductive rates.

To examine this result in greater detail, a more extensive series of simulations was carried out from $\beta = 0$ to $\beta = 2$ in increments of 0.02 for reproductive rates of $R = 50, 500$, and 950. This allowed for high-resolution examination of variation in evolved environmental tolerance levels at three horizontal transects across the surface of Figure 7(a). Figure 8(a) shows these transects as raw simulation output (median tolerance levels) with curves fitted via a robust LOESS procedure with 25% span; Figure 8(b) shows the fitted LOESS curves relative to a baseline in which half the



(a) (b)

Figure 7. (a) shows the median value at Locus 2 (tolerance or niche breadth) under each combination of noise colour and reproductive rate. (b) shows population diversity at Locus 1 (measured as the distance between the 2.5th and 97.5th percentiles of the population) under each combination of noise colour and reproductive rate. Both plots show medians over the last 8,000 iterations of each simulation run.

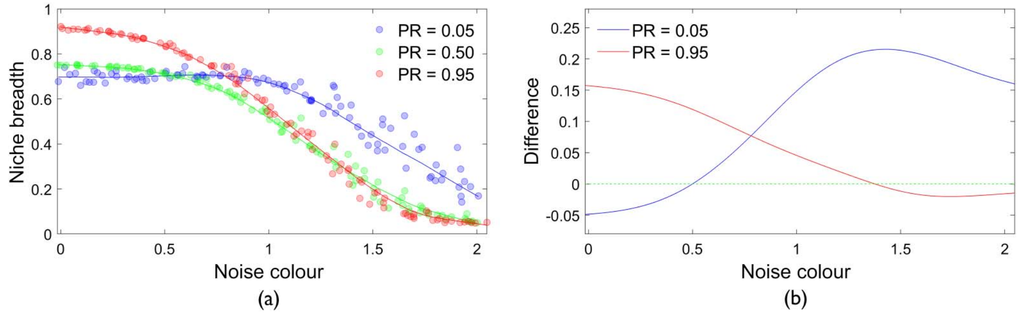


Figure 8. Higher resolution simulations of evolved niche breadth across a range of noise colours for three reproductive rates. (a) shows raw simulation output with fitted robust LOESS curves using a 25% span. (b) shows the resulting LOESS curves plotted relative to a baseline in which half the population is replaced each iteration (shown by the green line in (a)). PR = proportion of agents replaced each iteration.

population is replaced each iteration ($R = 500$). Figure 8 emphasizes the fact that conclusions drawn from a simulation employing white noise ($\beta = 0$) would be the opposite of the conclusions drawn from a simulation employing the more realistic pink noise (the transition from higher reproductive rates generating higher levels of tolerance to higher reproductive rates generating lower levels of tolerance occurs at $\beta \approx 0.8$). These results demonstrate not only that noise colour influences evolved levels of environmental tolerance but also that the interaction between noise colour and reproductive rate produces complex, nonlinear patterns in the response of this important evolutionary variable.

As shown in Figure 7(b), the diversity of values at Locus 1 increases markedly with reproductive rate under relatively white noise, but shows relatively little variation under reddened noise ($\beta > 1.6$). Diversity at Locus 2 (not shown) follows a very similar pattern. This result demonstrates that the effect of reproductive rate on population diversity depends heavily upon the colour of the environmental noise experienced by the population; simulations employing white noise would produce results qualitatively different from those employing the pink to red noises found more frequently in natural ecological and environmental settings.

4 Discussion

The results presented above highlight that the colour of noise chosen to represent the environment to which agents are adapting has a profound influence on model output. Gaussian (white noise) and Brownian (red noise) signals are found to represent the two extremes of a wide spectrum of noise colour variation, with the former eliciting selection for specialism, the latter generalism, and pink noise a balance between the two. We also found a complex non-linear interaction between the reproductive rate of the agents in a simulation and noise colour. Widely divergent and somewhat contradictory responses in niche breadth and population diversity are reported when applying these two most frequently used models for environmental signals to simulated populations with differing life histories. Together, this highlights the need to give serious consideration to the colour of noise applied in evolutionary simulations.

As originally reported in Grove et al. (2020), these results show that whiter environments generally require greater levels of environmental tolerance than those that exhibit redder power spectral densities, demonstrated by Figure 4. This result is closely related to the geometric mean effect in evolutionary biology, which states that under high levels of environmental variability (indicated here by environments with white power spectral densities), selection acts to reduce the variance in fitness over generations, even if this entails the sacrifice of highly fit individuals within any given generation (Lewontin & Cohen, 1969; Phillipi & Seger, 1989; Simons, 2002). At macro-evolutionary timescales, natural selection favours lineages with low variance in fitness over time rather than those with high instantaneous fitness at any given time; put simply, in a highly variable environment high fitness today may mean low fitness tomorrow, whereas moderate fitness today may equate to moderate fitness tomorrow (Figure 5). This is particularly true of white noise environments, due to their lack of autocorrelation; in a white noise environment, today's conditions are completely unrelated to tomorrow's conditions. In a red noise environment, by contrast, today's conditions act as at least a partial guide to tomorrow's conditions. The unpredictability of white noise leads logically to the evolution of greater generalism or tolerance, as this is the only strategy available when there are no available cues to future conditions.

The above is coherent with Potts' (1996, 1998, 2013) variability selection hypothesis, which argues that organisms develop greater versatility under varying conditions in order to deal with novel and unpredictable environments in the future. Potts (1998) draws evidence from hominin evolution, noting that key physiological and behavioural adaptations seem to have emerged in the hominin lineage during times of heightened variability. Paleoenvironmental data from the archaeological site of Olorgesailie reveal that whilst long-term evolutionary trends such as orbital cycles are detectable, there is also strong evidence of significant abrupt fluctuations in climatic conditions; this suggests a balance between low-frequency (≈red) oscillations and high-frequency (≈white) variability. If variability is considered to be the white noise component of a signal, then our results show support for the variability selection hypothesis; however, a more complex pattern in the behavioural response to environmental noise is reported above, requiring a careful consideration of the type of noise assumed when simulating evolution in response to environmental change.

Figure 7(a) demonstrates that all simulated populations, regardless of reproductive rate, evolve greater environmental tolerance under whiter noise; this is the primary output of the analyses conducted above. However, the analyses also demonstrate an intriguing interaction with reproductive rates in that under white noise, higher reproductive rates lead to greater levels of environmental tolerance, whereas under red noise, higher reproductive rates lead to lower levels of environmental tolerance. This latter result is made explicit by the analyses presented in Figure 8. As white noise and red noise are the two most widely used forms of environmental fluctuation in stochastic simulation models, the fact that they produce contrasting results in this regard suggests that more caution is needed when interpreting the results of such models, and that more focus is needed to establish the most appropriate form of environmental fluctuation for a given application.

It has been hypothesised that organisms with short life histories (and fast reproductive rates) are less likely to exhibit signs of behavioural versatility and instead are likely to track environmental fluctuations via genetic mechanisms (Grove, 2017; Grove et al., 2020). Encephalisation facilitates behavioural versatility (Reader & Laland, 2002; Street et al., 2017), and, whilst standard life-history theory in terms of the *r*/*K* division (Pianka, 1970; MacArthur & Wilson, 1967) does not directly consider the relationship between encephalisation and reproduction rate, brain and body size are tightly correlated in mammals (Herculano-Houzel et al., 2015; Jerison, 1975; Tsuboi et al., 2018). Indeed, many studies have suggested that brain size is in fact a more likely determinant of life-history variation than is body size (e.g., Barrickman et al., 2008; Deaner et al., 2003; Isler & van Schaik, 2009a,b). This makes sense in light of the expensive tissue hypothesis (Aiello & Wheeler, 1995), as the energy required to grow and maintain a large brain may have elicited a reduction in the energy allocated to reproduction (Isler & van Schaik, 2009a). Animals with lower reproductive rates have, on average, smaller brains when compared to related taxa with longer generational times (Grove, 2017), and relatively large-brained mammals show reduced annual fertility (Isler & van Schaik, 2009a). Over the past five million years, empirical paleoenvironmental data have shown a steady increase in variability (Lisiecki & Raymo, 2005), likely playing a key role in the increasing versatility observed in the hominin behavioural record, as proposed by the variability selection hypothesis. As human ancestors evolved slower life histories and larger brains, they would have become more dependent on cultural rather than biological evolution to adapt to environmental challenges.

Reproductive rates are inherently linked to evolutionary rates in sexually reproducing organisms; as recombination events are a major source of genotypic variation, species with faster reproductive rates produce more variation per unit time. The rate of molecular evolution varies consistently with life history parameters such as generation time across a wide range of mammalian taxa (e.g., Bromham, 2011). Elevation of the mutation rate itself—not directly explored in the above analyses—would be expected to produce an effect similar to an increase in reproductive rates (and mutation rate alone governs evolutionary rates in asexually reproducing organisms). Whilst higher mutation rates may permit faster evolution in a lineage, however, the vast majority of mutations are deleterious to individuals, and thus selection for increases in mutation rate is considered to be exceptionally rare (e.g., Kimura, 1967). Selection for faster or slower life history, by contrast, depends on a complex series of trade-offs; for example, a faster life history may be associated with greater fecundity but lower survivorship, and numerous life history strategies may lead to equivalent fitness (in the sense of the number of offspring surviving to reproductive age). The traditional dichotomy between investment in offspring quantity (*r*-selection) in variable environments and investment in offspring quality (*K*-selection) in stable environments may not be sufficient in cases where sexual maturity is delayed by substantial energetic investment in brain development, with individual and social learning subsequently employed to provide solutions to the challenges posed by environmental variability.

The results reported above agree with those of Halley (1996) that pink noise (broadly construed) is likely the most appropriate model of typical environmental noise for understanding long-term evolutionary dynamics. Both the niche breadth and the population diversity responses, depicted in Figure 7, are most consistent with standard life history theory under pink noise scenarios, with populations with higher reproductive rates exhibiting traits of specialists and populations with lower reproductive rates exhibiting traits of generalists. Animal population dynamics typically exhibit pink noise at a level that appears to be greater than would be expected from the environmental noise that the populations are exposed to. As demonstrated by Grove et al. (2020), these results show that pink noise is the pivot around which a change from high environmental tolerance (under white noise) to low environmental tolerance (under red noise) occurs, offering a critical balance between the need for plasticity during periods of high variability and to track longer-term environmental changes.

4.1 Conclusion

Our simulations suggest that populations evolving under increasingly reddened environmental regimes will tend to be more specialised, with narrower niches and a lower tolerance of environmental variability. This is due to the higher autocorrelation of redder relative to whiter noise, which leads in turn to redder environments being more predictable. However, there exists a complex interaction between noise colour and reproductive rate: Populations experiencing relatively white noise evolved greater environmental tolerance under higher reproductive rates, whereas populations experiencing relatively red noise evolved lower environmental tolerance under higher reproductive rates. Thus, conclusions drawn from simulations employing white noise would be the opposite of those drawn from simulations employing red noise. Further to this, the effect of reproductive rate on population diversity also depends heavily upon the colour of the environmental noise experienced by the population. It is recommended that future simulations should be conducted using a wider range of coloured noise models and that, where related empirical data are available, these should be analysed to determine the power spectral density of the environment being studied. This should ensure that simulation results are genuinely representative of both environmental and evolutionary dynamics.

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