

# Population dynamics and the colour of environmental noise

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## SUMMARY

The effect of red, white and blue environmental noise on discrete-time population dynamics is analysed. The coloured noise is superimposed on Moran–Ricker and Maynard Smith dynamics, the resulting power spectra are then examined. Time series dominated by short- and long-term fluctuations are said to be blue and red, respectively. In the stable range of the Moran–Ricker dynamics, environmental noise of any colour will make population dynamics red or blue depending on the intrinsic growth rate. Thus, telling apart the colour of the noise from the colour of the population dynamics may not be possible. Population dynamics subjected to red and blue environmental noise show, respectively, more red or blue power spectra than those subjected to white noise. The sensitivity to differences in the noise colours decreases with increasing complexity and ultimately disappears in the chaotic range of the population dynamics. These findings are duplicated with the Maynard Smith model for high growth rates when the strength of density dependence changes. However, for low growth rates the power spectra of the population dynamics with noise are red in stable, periodic and aperiodic ranges irrespective of the noise colour. Since chaotic population fluctuations may show blue spectra in the deterministic case, this implies that blue deterministic chaos may become red under any colour of the noise.

## 1. INTRODUCTION

The controversy on the existence and detection of complicated dynamics in natural populations (May 1974, 1976) is gaining colour. Population dynamics data of individual species are observed to be white or red (Sugihara 1995; Halley 1996). The colour refers to the analogy with the wavelengths in light. A time series is said to be white when no frequency dominance occurs, red when the population dynamics are dominated by low-frequency fluctuations, and blue when the population fluctuations are dominated by high-frequency oscillations. Thus, empirical observations in ecology give rise to the expectation that theoretical population dynamics models also produce patterns showing dominance of low frequencies (Pimm 1991; Powel & Steele 1995), i.e. such dynamics show reddish spectra.

The opposite was observed, however, when Cohen (1995) analysed chaotic dynamics of eight one-dimensional nonlinear population models. He showed that high frequencies dominate chaotic fluctuations in these models, contrary to expectation, making the power spectra blue. In an early reaction, Sugihara (1995) suggested that natural population fluctuations are not chaotic and/or non-stationary, the models are fundamentally flawed, or environmental

forcing needs to be incorporated. These findings were soon commented on by a number of authors (Blarer & Doebeli 1996; Kaitala & Ranta 1996; White *et al.* 1996). Blarer & Doebeli (1996) argued that Cohen (1995) reported results that are based on a limited number of parameter values in each model. They showed importantly that in these models the spectrum of chaotic dynamics may change for different parameter values. In particular, increasing the growth rate in the Moran–Ricker model may whiten the occasionally blue spectrum. More generally, they showed that density dependence may have a profound effect on the colour of the population dynamics. White *et al.* (1996) argued that adding a spatial dimension to the population dynamics will give rise to reddened spectra while Kaitala & Ranta (1996) reported that delayed density dependence (Turchin 1990; Ranta *et al.* 1995; Kaitala *et al.* 1996) will remove the dominance of high-frequency oscillations and will either whiten or redden the frequency distribution of the population dynamics.

The role of environmental forcing, or noise, was not touched upon in the previous refined analyses, perhaps mainly because it is known that environmental noise may affect the colour of the population dynamics (Sugihara 1995). For example, environmental

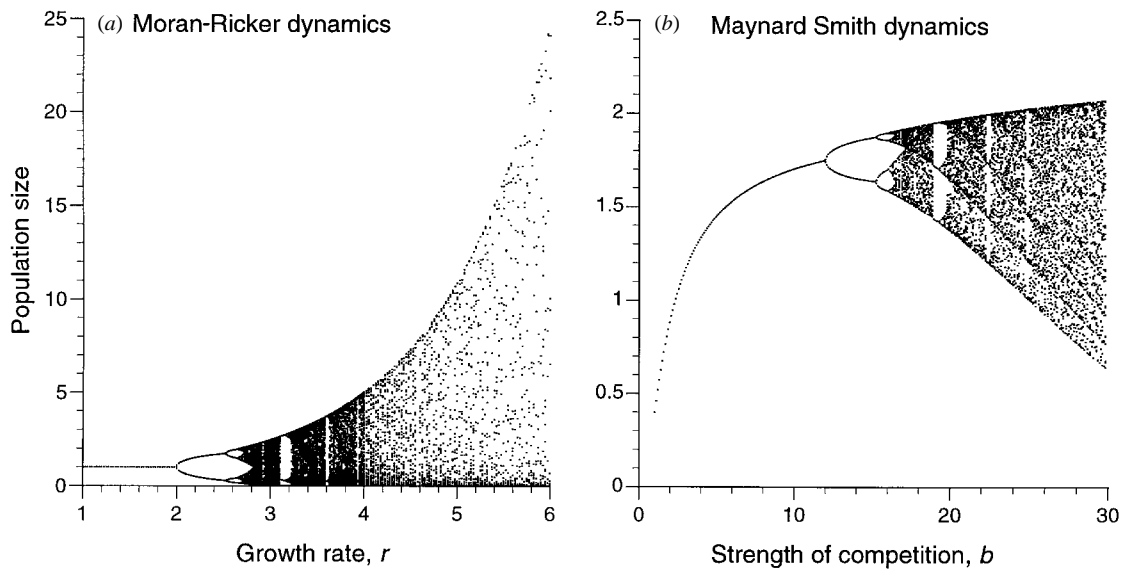


Figure 1. Bifurcation diagrams describing the deterministic population dynamics produced by: (a) the Moran–Ricker model; and (b) the Maynard Smith model in the absence of environmental noise. In the simulations, the first 200 values of population sizes were omitted to remove the initial transient and the next 100 values were printed for each  $r$  in panel (a) and for each  $b$  in panel (b). The initial population sizes were randomly and uniformly distributed between 0 and 1. In panel (b)  $a = 0.5$  and  $r = 1.2$ .

forcing can push a stable map into a chaotic regime (Rand & Wilson 1991; Sugihara 1994). It has also been suggested that red environmental noise, superimposed on models containing multiple stable states, may tinge power spectra with red (Steele 1985). However, we show that the effect of environmental noise upon population dynamics has not yet been fully explored.

Here we analyse the effects of environmental noise on stable, cyclic and chaotic population dynamics produced by Moran–Ricker and Maynard Smith models. We show that environmental noise may crucially affect the colour of population dynamics. In particular, adding white noise to stable population dynamics will make the population dynamics either red or blue, depending on the value of the population growth rate (Moran–Ricker model) and the type and strength of density dependence (Maynard Smith model). Population dynamics that are subjected to red and blue environmental noise show, respectively, more red or blue power spectra than those subjected to white noise. However, the sensitivity to the differences in the environmental colours decreases with increasing complexity of the dynamics and ultimately disappears in the chaotic range of the population dynamics. In the chaotic range of the Maynard Smith model an environmental noise of *any* colour may make blue deterministic dynamics red.

## 2. MORAN–RICKER MODEL AND ENVIRONMENTAL NOISE

We use the well-known Moran–Ricker discrete-time nonlinear population model (Moran 1950; Ricker 1954)

$$P_{t+1} = P_t f(P_t), \quad (1)$$

where  $t = 0, 1, 2, \dots$  and  $P_t$  denotes the population size at time  $t$ . The density dependence in equation (1) is defined as

$$f(P_t) = \exp[r(1 - P_t)], \quad (2)$$

where  $r$  is a constant density-independent growth rate. The deterministic population dynamics of the Moran–Ricker model are stable for  $r < 2.0$ , for  $2.0 < r < 2.6924$  there is a period-doubling route to chaos (May 1976), and for  $r > 2.6924$  a chaotic region including periodic windows (figure 1a).

In our simulations we subjected the population dynamics to environmental noise having different colours. For brevity we assume a multiplicative effect of the noise yielding the following population dynamics:

$$P_{t+1} = P_t f(P_t)(1 + d_t), \quad (3)$$

where  $d_t$  is a coloured environmental noise generated by

$$d_{t+1} = cd_t + w_t, \quad (4)$$

where  $w_t$  is a random variable (i.i.d., uniformly distributed on the interval  $(-0.5, 0.5)$ ). This process yields power spectra of the coloured noise as red, white and blue for  $c$  greater than, equal to and less than zero, respectively. All the simulations were carried out by applying the values  $c = 0.4, 0$  and  $-0.4$ , corresponding to red, white and blue spectra (figure 2a; for the computation of a power spectrum, see, for example, Cohen 1995).

To further the examination of the significance of the colour of the noise in affecting population dynamics we carried out a more detailed analysis in the regions of  $r$  resulting in stable, periodic and chaotic dynamics. This classification is based on the stability properties of deterministic dynamics (figure 1a).

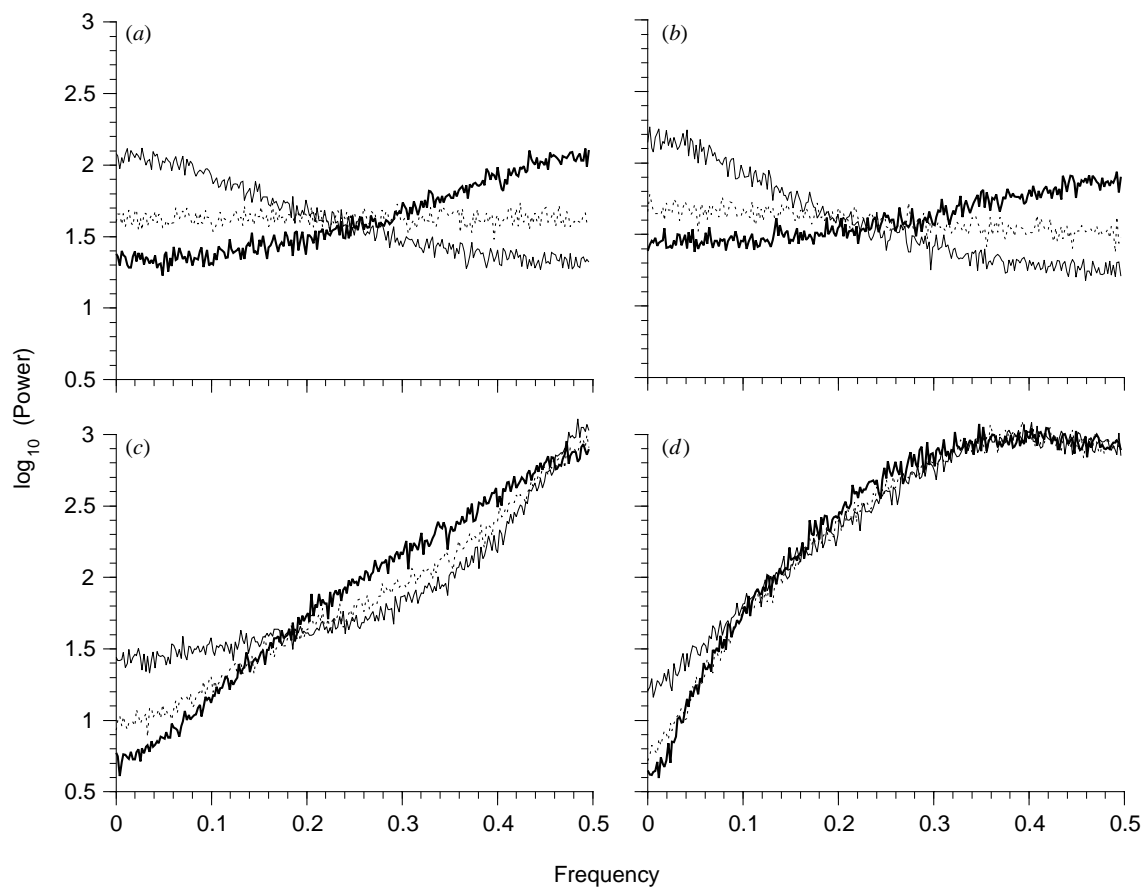


Figure 2. (a) Power spectra of the red, white and blue noises. (b) Sample power spectra of the population dynamics for  $r = 1.0$  when subjected to white, red and blue environmental noise, respectively. Sample power spectra for (c),  $r = 2.3$  and (d),  $r = 3.0$ . Power spectra are averages of 100 simulations in all panels. Notation: thick full lines, blue; thin dashed lines, white; thin full lines, red environmental noise, respectively.

Note that we do not claim that the population dynamics maintain their stability properties when subjected to different classes of environmental noise. Sugihara (1994) showed, for example, that a noise-driven originally stable logistic population dynamics may show chaotic behaviour. These considerations are, however, beyond the scope of this paper.

#### (a) Stable population dynamics

By definition, asymptotically stable deterministic population dynamics converge exponentially to an equilibrium population level, which is represented in the bifurcation diagram by a single point (figure 1a). For stable population dynamics the power is zero for positive frequencies. However, when environmental noise is added, stable population dynamics start oscillating around the equilibrium population. Figure 2b shows the power spectra of the population dynamics for  $r = 1.0$  when influenced by white, red and blue environmental noises. Thus, white environmental noise produces a white spectrum, and red and blue noises produce red and blue power spectra, respectively. In other words, the colour of the environmental noise is transmitted to the population dynamics when the population is inherently stable.

However, the effect and the colour of the power spectra are not independent of the specific value of

the growth rate,  $r$ , within the stable area. We used colour index (Blarer & Doebeli 1996) to study this question. Colour index is defined as the ratio between the area under the spectrum ranging from 0–0.25 to the area ranging from 0.25–0.5. With red spectra the index assumes values greater than one, with white spectra these two areas are largely matching, while with blue spectra the index values are less than one.

We observe that in the region of stable dynamics ( $r < 2.0$ ) of the Moran–Ricker model the value of the intrinsic growth rate,  $r$ , affects crucially the colour of the population dynamics when the population dynamics are subjected to an environmental noise of any colour (figure 3a): the population dynamics with low growth rates are typically red, turning blue with increasing growth rate. Red population dynamics are observed for low values of  $r$  even for white and blue environmental noises, and blue population dynamics are observed for higher values of  $r$  even for white and red environmental noises. In particular, we do not need multiple attractors to observe the crucial effect of the environmental noise on the colour of the population dynamics as discussed by Steele (1985). However, the colour of the environmental noise seems to be important for ‘intermediate’ growth rates around  $r = 1.0$ .

The reason for the power spectra becoming blue with increasing growth rate,  $r$ , is probably the fact

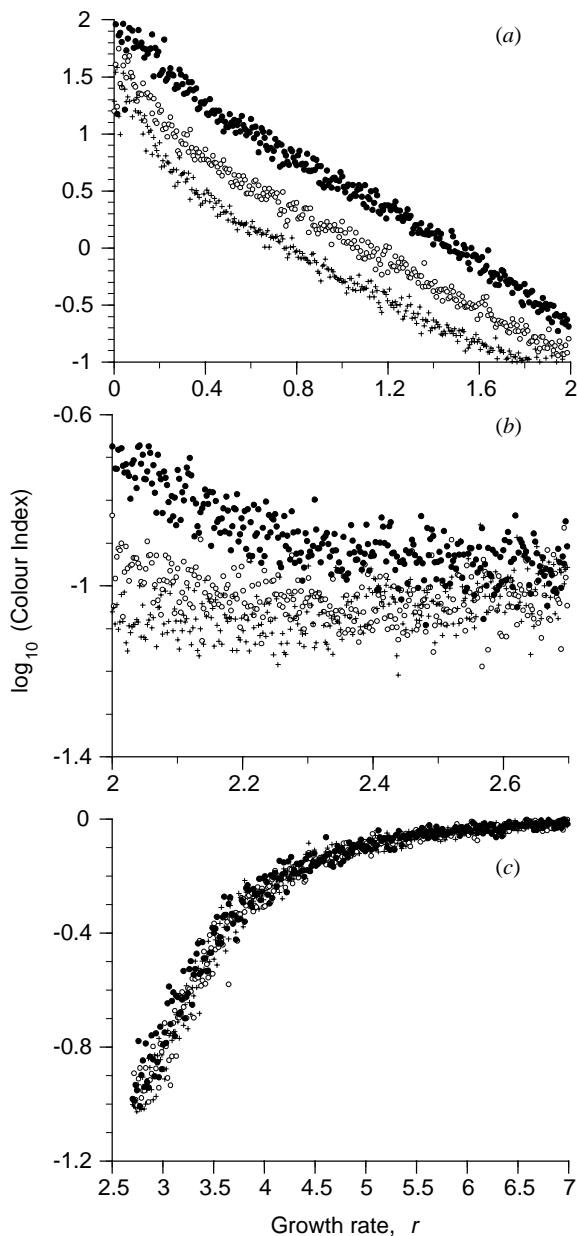


Figure 3. The logarithms of the values of the colour indices as a function of the intrinsic growth rate  $r$ : (a) over the stable region; (b) over the period-doubling cascade to chaos; and (c) in the chaotic range. Positive and negative values indicate red and blue colours, respectively. In all panels we have used 300 equally spaced values of  $r$ . Notation: +, blue; o, white; and ●, red environmental noise, respectively.

that when  $r$  increases we gradually approach the bifurcation point  $r = 2.0$ , at which the stable undisturbed population dynamics bifurcate and turn to periodic population dynamics. The loss of stability with increasing growth rate is reflected in the colour index at each value of  $r$ . This can be understood as follows. The derivative of function  $P_t f(P_t)$  at the equilibrium  $P = 1$  (i.e. the eigenvalue of the linearized system) is  $\lambda = 1 - r$ . Thus, we have  $0 < \lambda < 1$  for  $0 < r < 1$  and  $-1 < \lambda < 0$  for  $1 < r < 2$ . In the first case the convergence of the population dynamics to the equilibrium state is exponential while in the latter case the convergence includes oscillations. These

different types of approaches to equilibrium could cause the colour of population dynamics subjected to environmental noise. The non-oscillatory exponential approach to equilibrium suggests positive autocorrelations in the time series, and therefore the dominance of the long-term trends and reddened spectra are expected. The oscillatory approach, however, implies negative autocorrelations and, thus, blue spectra.

We observe that, for each value of the intrinsic growth rate  $r$ , the colour of the population dynamics is affected by the colour of the environmental noise: red and blue environmental noises cause, respectively, red and blue shifts in the colour of the population dynamics, as compared to the colour under white noise. Thus, stable population dynamics are sensitive to the colour of the environmental noise.

#### (b) *Period-doubling route to chaos*

We next study the interval of the growth rates on which the period-doubling route to chaos occurs. Our simulations show (figure 3b) that the power spectra remain blue for the whole interval of the period-doubling cascade ( $2.0 < r < 2.6924$ ). Nevertheless, oscillations with low period appear to be sensitive to the colour of the environmental noise in the sense that the difference of the colour of the environment can be observed for  $2.0 < r < 2.4$ . It is interesting to note, however, that the sensitivity to the differences in the environmental colour vanishes as the dynamics approach the chaotic region with increasing  $r$  (figure 3b).

As an example we calculated the power spectra for  $r = 2.3$  (figure 2c). Although the colour index does not seem to differ much among the differently coloured environmental noises the power spectrum induced by red environmental noise follows more closely that of white noise for the higher frequencies ( $f > 0.175$ ) than does that of the blue noise. The pattern is revised at the low frequencies ( $f < 0.175$ ): the power spectrum induced by blue noise follows more closely that of white noise than does that of the red noise.

#### (c) *Chaotic population dynamics*

For  $r > 2.6924$  the population dynamics turn to chaos. As above, we ask whether the differences in the colour of the noise can be observed in the colour of chaotic dynamics? We see that the difference between the different colours of the environmental noise seems to be minor, as compared with the differences observed for the stable and periodic regions of the population dynamics. Furthermore, the colour of the power spectrum approaches that of white, irrespective of the colour of the environmental noise (figure 3c). This observation is in accordance with Blarer & Doebeli (1996). For  $r = 3.0$  we observe clear differences among the power spectra only at very low frequencies (figure 2d).

To finish with we pose a more detailed statistical question: is it possible to make a difference among

the colour indices over the whole range of  $r$ ? The answer is dependent upon the range of the growth rate coefficient,  $r$ , adopted. To us there are three natural breaking points in  $r$ : the range of stable dynamics (figure 3a), the range of period doubling (figure 3b) and the range of chaotic dynamics (figure 3c). Running the analysis of covariance, ANCOVA (colour of the noise as categorical variable, growth rate  $r$  as covariate) for the range of stable population dynamics yields  $F_{2,894} = 9.38$  ( $p < 0.001$ ) for the equality of slopes tests. This indicates the less obvious, that the slopes of the three noise colours are different in statistical terms. Furthermore, the colour indices assume values at different levels ( $F_{2,894} = 870.61$ ,  $p < 0.001$ ) for the differently tinged noise (figure 3a). The differences are even more pronounced at the period-doubling range of  $r$  (equality of slopes  $F_{2,894} = 303.58$ ,  $p < 0.001$ ; equality of covariate adjusted means  $F_{2,894} = 392.29$ ,  $p < 0.001$ ; figure 3b). On the contrary, no such differences were found at the chaotic range of  $r$  (equality of slopes  $F_{2,894} = 1.84$ ,  $p = 0.159$ ; equality of covariate adjusted means  $F_{2,894} = 2.12$ ,  $p = 0.121$ ; figure 3c).

### 3. MAYNARD SMITH MODEL

In order to obtain a more general picture of the interaction between environmental noise and population dynamics we also analysed the more sophisticated Maynard Smith model (Maynard Smith 1974). Here the density dependence (see equation (1)) is defined as

$$f(P_t) = r/(1 + (aP_t)^b), \quad (5)$$

where  $r$  is the growth rate,  $a$  scales the carrying capacity and  $b$  describes the type and strength of density dependence. The environmental noise was added as in the Moran–Ricker model (equations (3) and (4)).

Parameters  $r$  and  $b$  affect the dynamics of the Maynard Smith model. When  $r$  is constant and  $b$  increases, stable dynamics become first periodic and then chaotic (figure 1b). Increasing  $r$  also increases the complexity of the dynamics.

For high fixed values of growth rate (e.g.  $r = 6.0$ ) red colour can be observed both in the stable and chaotic ranges of  $b$  (figure 4b). Blue spectra are observed for  $1.5 < b < 9$ , that is, around the values of  $b$  producing period-doubling cascade to chaos. As in the Moran–Ricker model the dynamics are sensitive to the differences in the environmental colours in the stable and cyclic range but not in the chaotic range.

For a low value of the growth rate ( $r = 1.2$ ) the power spectra are red for all values of  $b$ , that is, for stable, periodic and chaotic ranges, and for all environmental colours considered (figure 4a). Blarer & Doebeli (1996) observed that for strong density dependence (i.e. large values of  $b$ ) and low growth rate  $r$ , the colour of the deterministic Maynard Smith dynamics is red. Note that the colour of the deterministic chaotic dynamics is blue for  $r = 1.2$  in the early part of the chaotic range. Thus, interestingly enough,

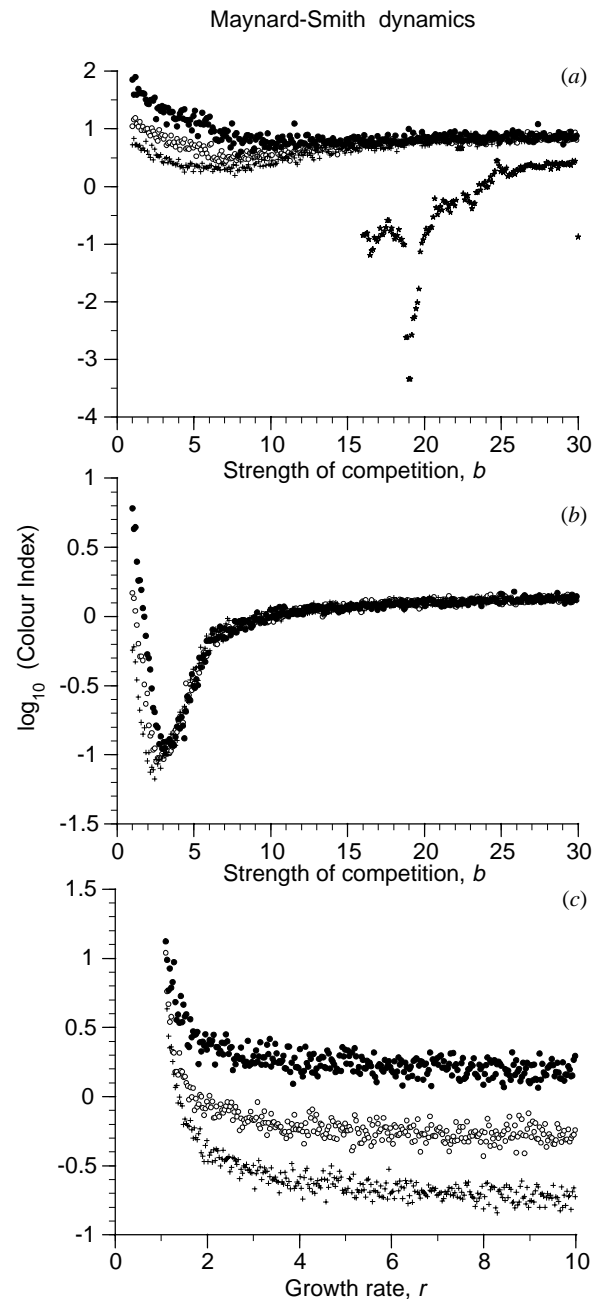


Figure 4. The colour indices corresponding to red, white and blue noises in the Maynard Smith dynamics as a function of  $b$  when growth rate is constant: (a)  $r = 1.2$ ; and (b)  $r = 6.0$ . (c) The colour indices as a function of  $r$  when the derivate at equilibrium is kept constant:  $\lambda = -0.25$ . We have used 300 equally spaced values of  $b$  and  $r$ .  $a = 0.5$ . Notation: +, blue; o, white; and ●, red environmental noise, respectively, and \*, the colour of the undisturbed chaotic dynamics for  $r = 1.2$ .

blue environmental noise can make blue chaotic dynamics red. However, the opposite—red dynamics turning to blue—was not observed.

One would expect that when the complexity of the dynamics is maintained constant the effects of environmental noise would be unchanged. We studied this question in the stable region of the Maynard Smith model by maintaining the derivate at the equilibrium constant but changing the values of  $r$  and  $b$ . Figure 4c shows the colour indices corresponding to

red, white and blue noises for the constant derivate at equilibrium  $\lambda = 1 - b + b/r = -0.25$ . As  $r$  is increased then  $b$  is decreased, which affects the strength of density dependence in the model. The results show that although the equilibrium population size of the undisturbed model remains equally stable the disturbed dynamics may be blue or red.

As a whole, the analysis of the Maynard Smith model completes the picture obtained above from the Moran–Ricker model. When different environmental colours are added to the models, low growth rates tend to produce red dynamics. Furthermore, red and blue environmental noises produce, respectively, more red and blue power spectra as compared to white environmental noise in the stable range of the dynamics, whereas the differences disappear when the complexity of the dynamics increases. The analysis of the Maynard Smith model shows that the stability properties of the model do not alone determine the colour of the dynamics under environmental noise—different combinations of growth rate and density dependence may produce qualitatively different results. Furthermore, the colour of the disturbed dynamics may be red for all ranges of stability (stable, cyclic and chaotic) of the dynamics, and blue chaotic dynamics may turn to red under the influence of environmental noise of any colour.

#### 4. CONCLUSIONS

We have analysed the effects of the colour of environmental noise on population dynamics that range from stable via cyclic to chaotic behaviour. We have shown that environmental noise may well affect the colour of population dynamics. Not entirely unexpectedly, red and blue environmental noises increase, respectively, the presence of long- and short-term fluctuations in the population dynamics in the stable range of population dynamics. However, it is not possible to derive the colour of the environmental noise from the colour of the population dynamics alone. Subjecting stable population dynamics to white environmental noise is observed to induce either red or blue population dynamics, depending on the value of the intrinsic growth rate and the type and strength of density dependence or intraspecific competition. The difference between the effects of the environmental colours decreases with increasing complexity of the dynamics and disappears in the range of chaotic population dynamics. In the chaotic range of population dynamics environmental noise may have an unexpected effect on the undisturbed dynamics: blue dynamics may become red under disturbances of any colour.

The models that we used in our study are robust in the sense that small changes in the amplitude of environmental noise do not change the results qualitatively. Furthermore, introducing the environmental noise directly into the exponential ‘fitness function’

of the Moran–Ricker model ( $f(P_t)$ , see equation (2)), either in the multiplicative or additive form, does not affect our main conclusions.

We concentrated in this article on two single-species models with non-delayed density dependence. The effects of spatial structure, population interactions or different patterns of density dependence on the sensitivity of population dynamics to the colour of the environmental noise remain unknown.

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