

Is the impact of environmental noise visible in the dynamics of age-structured populations?

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Climate change has ignited lively research into its impact on various population-level processes. The research agenda in ecology says that some of the fluctuations in population size are accountable for by the external noise (e.g. weather) modulating the dynamics of populations. We obeyed the agenda by assuming population growth after a resource-limited Leslie matrix model in an age-structured population. The renewal process was disturbed by superimposing noise on the development of numbers in one or several age groups. We constructed models for iteroparous and semelparous breeders so that, for both categories, the population growth rate was matching. We analysed how the modulated population dynamics correlates with the noise signal with different time-lags. No significant correlations were observed for semelparous breeders, whereas for iteroparous breeders high correlations were frequently observed with time-lags of -1 year or longer. However, the latter occurs under red-coloured noise and for low growth rates when the disturbance is on the youngest age group only. It is laborious to find any clear signs of the (red) noise- and age group-specific fluctuations if the disturbance influences older age groups only. These results cast doubts on the possibility of detecting the signature of external disturbance after it has modulated temporal fluctuations in age-structured populations.

Keywords: noise; population dynamics; age structure; Leslie matrix; external disturbance

1. INTRODUCTION

Recent concern about warming of the global climate (e.g. Ropelewski & Jones 1987; Hurrell 1995; Trenberth & Hoar 1996; Dai *et al.* 1998) has stimulated an approach to associating observed ecological time-series with climate indices such as the North Atlantic Oscillation (NAO). The scope in this research agenda is to correlate (possibly with time-lags) one of the global climate indices with extant long-term population data. Most often this has been done with the NAO and statistically significant correlations (or nearly so) have been reported for a great variety of taxa. These deal mostly with aquatic organisms (Reid 1978; Friedland *et al.* 1993; Fromentin & Planque 1996; Alheit & Hagen 1997; Dippner 1997; Kröncke *et al.* 1998; Reid *et al.* 1998; Tunberg & Nelson 1998; Belgrano *et al.* 1999), but there are also examples from terrestrial ecosystems (Schmitt 1983; Galen & Stanton 1991; Leirs *et al.* 1997; Forchhammer *et al.* 1998; Grenfell *et al.* 1998; Lima *et al.* 1999; Post & Stenseth 1999; Post *et al.* 1997, 1999; Saether *et al.* 2000).

Although the above list is not complete, it does however serve as an indication that the search for a statistical association between population data and climatic fluctuations is recent and keen. However, it is worth mentioning that the climate change research agenda, when studied at the population level, ties back to the old debate on the relative merits of density-independent and density-dependent processes being responsible for population fluctuations (Andrewartha & Birch 1954; Lack 1954; Turchin 1999). Research on game animal dynamics is littered with suggestions that short-term population fluctuations find their explanations in weather and climate

factors (Siivonen 1956, 1957; Arditi 1979; Slagsvold & Grasaas 1979; Schröder *et al.* 1982; Eiberle & Matter 1984, 1985a,b; Steen *et al.* 1988; Swensson *et al.* 1994). This is because of an appeal for finding rational explanations for the effect of weather-derived variables and how they may influence population fluctuations via births and deaths. This idea is in fact better known as the climate control theory (Bodeheimer 1938; Andrewartha & Birch 1954).

It is of interest to us to note that the road of the climate control theory is almost exclusively paved with empirical studies (including very recent ones) searching for statistical signs of an association between population data and external fluctuations (Royama (1977, 1992) and Lindström (1998) are exceptions with a theoretical orientation). Contrary to this but in concert with Ranta *et al.* (2000), we have decided to restrict ourselves to an endeavour where both the population renewal process and the external noise (used here as a synonym for long-term fluctuations in climate) are precisely known. This is in contrast to most other researchers, who are interested in how, for example, the NAO may modulate the population renewal process. The divergence in our starting point and the empirical data approach is that, in the empirical setting, often neither the population renewal process nor the modulating signal are known precisely enough.

We shall allow ourselves the luxury of knowing both the signal and the population dynamics fully. This is because, in statistical terms, we are interested in to what extent and under what conditions the modulated population data and the modulating signal are in any way associated. Thus, we are looking for visibility of the external noise in noise-modulated population fluctuations (Ranta *et al.* 2000; Laakso *et al.* 2001). For this purpose, we need

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to know the noise signal and the population dynamics without any bias after the noise has been filtered through the population renewal process. Our approach is thus free of sampling error (population data). We have also detected the signal modulating the renewal process of our target population with precision. We have a simple justification: if the signal and the signal-modulated population dynamics in our setting are not associated in any way, it is far more difficult, we believe, for the empirical approach to find a correlation between a perhaps unknown signal and extant population data.

2. AGE-STRUCTURED POPULATION DYNAMICS AND ENVIRONMENTAL FORCING

We take the population dynamics as obeying an age-structured renewal process after the Leslie (1945, 1948; Caswell 2001) matrix model

$$\mathbf{n}_{t+1} = \mathbf{V}_t \mathbf{M} \mathbf{n}_t, \tag{1}$$

where \mathbf{n}_t is a column vector giving the distribution of individuals in k age groups at time t and \mathbf{M} is a $k \times k$ matrix where the first row gives the age group-specific fecundities, F_i , where $i=0, \dots, k-1$, and the first subdiagonal indicates age group-specific survival probabilities, P_i , where $i=0, \dots, k-2$. Finally, \mathbf{V}_t is a $k \times k$ diagonal matrix where the diagonal elements represent the age group-specific environmental noise. The scalar variable (v_t) determining the diagonal values of \mathbf{V}_t (see below) is taken after a first-order autoregressive process (Ripa & Lundberg 1996), i.e.

$$v_t = \beta v_{t-1} + s\sqrt{1 - \beta^2}, \tag{2}$$

where β is the autocorrelation parameter ($-1 < \beta < 1$) or the colour of the noise (negative values refer to blue colour with short wavelengths dominating, positive values generate red noise with a dominance of long wavelengths and $\beta=0$ refers to white noise). The term s is a normally distributed random variable with mean equal to zero and variance equal to unity. We also truncated the values of the autoregressive process within the range $(1-w, 1+w)$ (we use $w=0.5$ throughout, but using other values of w ($0.05 < w < 0.8$) will give closely matching results as reported below). The square-root term scales the variance of the time-series generated so that its true variance is independent of β and the length of the time-series (Heino *et al.* 2000). When the noise affects only one age group, e.g. the first one, we take $\mathbf{V}(0,0)_t = v_t$ after equation (2) while $\mathbf{V}(1,1)_t$ to $\mathbf{V}(k-1, k-1)_t$ are all equal to 1. When more than one age class is affected the noise signals are identical for each age class.

We are not only interested in the visibility of the noise in the age-structured population dynamics, but also to what extent two life histories, namely iteroparity and semelparity (e.g. Roff 1992), give matching results. Iteropary refers to reproducing more than once in a lifetime, while semelparous breeders reproduce only once in their lifetime. Thus, equation (1) has to be modified in order to acknowledge this fact. For the iteroparous breeder we have

$$\mathbf{M}_I = \begin{bmatrix} F_0 & F_1 & \dots & F_{k-2} & F_{k-1} \\ P_0 & 0 & \dots & 0 & 0 \\ 0 & P_i & \dots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \dots & P_{k-2} & 0 \end{bmatrix}, \tag{3}$$

while the corresponding matrix for the semelparous breeder is

$$\mathbf{M}_S = \begin{bmatrix} 0 & 0 & \dots & 0 & F_{k-1} \\ P_0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & \ddots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \dots & P_{k-2} & 0 \end{bmatrix}. \tag{4}$$

Of course we also have \mathbf{n}_I and \mathbf{n}_S . The dominant eigenvalue of \mathbf{M} is λ , which is the geometric growth rate. Having both \mathbf{M}_I and \mathbf{M}_S , we selected the age group-specific fecundity values so that $\lambda_I = \lambda_S$. For the growth rate we used two values of $\lambda = 1.1$ and $\lambda = 3.0$ for a slowly growing population and a population with a faster growth rate, respectively. Here we shall report results for $k=10$ for the number of age groups (using another number for k does not change the major outcome provided that k is greater than or equal to 3).

We explored the effect of the external noise by calculating age group-specific cross-correlation coefficients CCF_i as $r_{\text{tag}}[\mathbf{n}(i)_t, \mathbf{V}(i,i)_t]$, where i is an age-group index (e.g. Chatfield 1984). We calculated CCF_i with time-lags of 0 to -10 years.

When equation (1) is iterated repeatedly the emerging dynamics is exponential growth. To make it a bit more realistic we modified it after Leslie (1948) in order to acknowledge the carrying capacity K (here $K=5000$). Leslie (1948) defined a quantity q_t representing the effect of density on the survival rate for each age group as

$$q_t = 1 + \left[\frac{\lambda - 1}{K} \right] N_t, \tag{5}$$

where $N = \sum \mathbf{n}$. By assuming that density only acts on the survival probabilities Leslie (1948) formed a diagonal matrix \mathbf{Q}_t with q_t in the diagonal. The effect of the carrying capacity is achieved by using

$$\mathbf{n}_{t+1} = \mathbf{V}_t \mathbf{Q}^{-1} \mathbf{M} \mathbf{n}_t \tag{6}$$

instead of equation (1).

We initialized \mathbf{n} with uniformly distributed random numbers (1,100) and iterated equation (6) with the matrices in equations (3) and (4) for 5000 generations in order to erase transient behaviour. The following 1000 time-units were used to score the CCF_i .

We tested the prediction that is implicitly included in the climate control theory, that environmental forcing drives population fluctuations such that its effect becomes clearly visible at least in some stages of the life cycle of an organism, using the model developed above. In a positive case, we should observe significant positive or negative covariance between environmental noise and the size of at least one cohort or age class. Moreover, it is often proposed that environmental forcing is a general property

such that it is independent of the life histories of organisms.

3. RESULTS

In our first exploration with $k=10$ we let the noise modulate the temporal dynamics of the numbers in the first age group and explored the correlation between the noise signal and \mathbf{n} with the cross-correlation technique (with time-lags from 0 to -10 years). We had blue noise ($\beta = -0.8$), white noise ($\beta = 0$) and red noise ($\beta = 0.8$) colours and the geometric growth rates were $\lambda = 1.1$ and $\lambda = 3.0$. To our great surprise the noise, as measured in terms of CCF_b , was found to be invisible with a semelparous (only the final age group reproduces) life history (figure 1). The second surprise is that, even with the iteroparous life history (reproducing several times per lifetime), the noise is by and large invisible when the population has a small growth rate ($\lambda = 1.1$). Blue and white noise are not detectable (figure 1*a,b,d,e*). When the dynamics are modulated by white noise one can find their signature in the population dynamics, but the signal is weak (figure 1*b*). With red noise and in iteroparous breeders one begins to see the noise in the temporal dynamics of the age groups very clearly. Of course, the signal is most clearly visible (with time-lags) in the dynamics of the age group the noise is modulating (figure 1*c*). With a higher population growth rate ($\lambda = 3.0$) the above conclusions are strengthened. Interestingly enough, with red noise the lagged correlations with noise and population data are positive for the first (noise hits here) and second age groups, while from the third age group onwards the noise signal and population dynamics correlate negatively (figure 1*f*).

We next limited our exploration to red noise only ($\beta = 0.8$) and examined the visibility of the noise when a matching external signal influences more than one age group at a time. For this purpose we used only the iteroparous life history with the age-group number being 10. When the signal was on the three first age groups its presence was obvious with appropriate time-lags (figure 2*a*). However, with $\lambda = 3.0$ the correlation between the signal and the modulated dynamics is also positive for the first four age groups but turns negative from the fifth group onwards (figure 2*b*). Detecting the signal in age groups from group 3 onwards presents no problem with noise modulating age groups 3–5, but seeing it in the first three age groups becomes more difficult, particularly with a high population growth rate (figure 2*c,d*). The same is more or less true with the noise hitting the three oldest age groups only (figure 2*e,f*). Only when all age groups are equally affected by the external disturbance do the possibilities of seeing the noise in the modulated dynamics improve drastically (figure 2*g,h*).

4. DISCUSSION

Based on the number of studies aiming to correlate population dynamics with environmental changes, one can derive a straightforward working hypothesis that environment is a modulator in population dynamics (Andrewartha & Birch 1954). It is tempting to suggest that the null expectation is that the qualitative properties

of the modulating noise are qualitatively transported to these dynamics. This is particularly the case when the principal tool in signal identification in population dynamics is linear correlation (with time-lags) between population fluctuations and the presumed noise modulating them.

Using an age-structured population model we have explored whether data on noise-modulated population dynamics can be correlated with an environmental time-series, which is interpreted here as an external noise signal affecting the quality of population dynamics. Our principal findings on the visibility of external noise in the dynamics of an age-structured population can be summarized as follows. First, no matter what, the noise remained invisible in the dynamics of a population obeying semelparous reproduction. Second, with an iteroparous life history, the visibility of the noise improves drastically with a high population growth rate and when the external noise is of red colour. With a slow population growth rate and when the noise only affects younger age groups its visibility decreases in the dynamics of older age groups. Increasing the growth rate makes younger age groups (the ones affected by the noise) correlate positively with the noise signal, while older age groups (which are not affected by the noise) will correlate negatively in their fluctuations with the noise signal. If the signal only affects older age groups it is not visible in the dynamics of the younger age groups. Only when the noise influences all extant age groups with equal efficiency does it become easily visible. These findings raise a few questions, some of which we can provide an answer for, while others will need to wait for more research to be performed. Third, blue noise and white noise are by and large invisible in the age-structured population data.

Why is the noise invisible in the population obeying a semelparous life history? The answer for this comes from the fact that semelparity, as modelled here, yields periodic dynamics with the dominating period matching the number of age classes (see Lindström *et al.* (1995) for more of the technical details). In periodic dynamics the skeleton signal of the population renewal process is so strong that it easily masks the impact of the external signal. This has also been shown by Ranta *et al.* (2000) using a linear second-order autoregressive process, i.e. AR(2). In the parameter range where AR(2) yields periodic dynamics the correlation between the external signal and the signal-modulated population dynamics was very low (r_{-1} ranged from 0.1 to 0.15; Ranta *et al.* 2000).

Why does the noise become more visible with an increasing growth rate? This finding is in contrast to our earlier results using Ricker dynamics for the population renewal process (Ranta *et al.* 2000). That the effect of the noise disappeared with the Ricker growth rate increasing from the stable region to the chaotic region is understandable. In the Leslie matrix approach the lower growth rate gives slower resonance to the disturbed dynamics, whereas with a higher growth rate the deviated population soon returns back to its original value and, once disturbed again, follows the external modulator more closely. The invisibility of blue and white noise follows the same explanation: now the noise is faster than the dynamics. These results appear to be highly relevant when assessing the strength of climatic forcing in population dynamics because species differ widely in

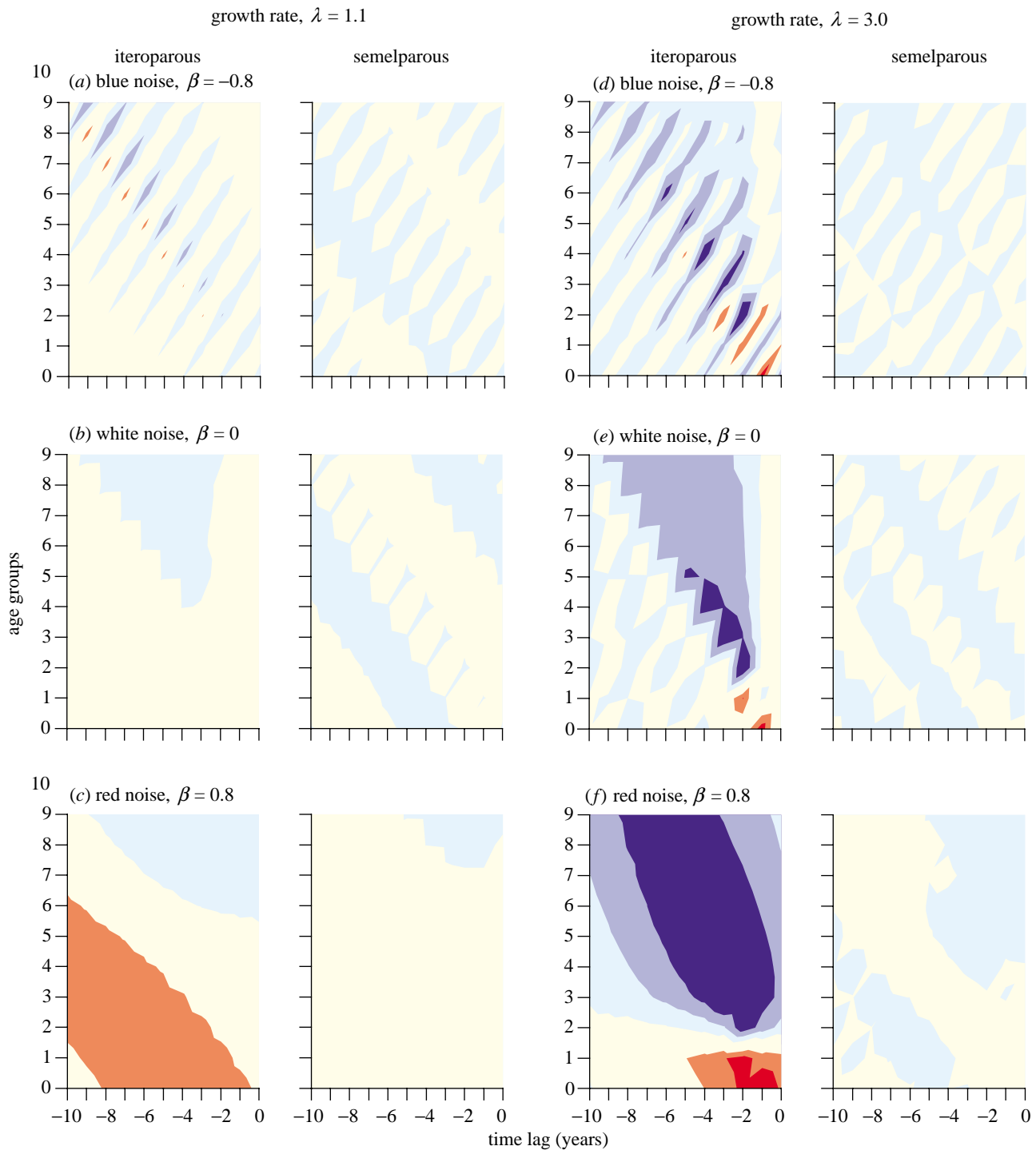


Figure 1. Age group- ($k = 10$) specific contour maps of the cross-correlation coefficients against various time-lags (from 0 to -10 years). The contour axis for the cross-correlation coefficient ranges from -1 to 1 with a step of 0.25 . Blue shades are for negative correlations (deep blue -0.75 to -1 and light blue -0.25 to 0) and shades from yellowish (0 – 0.25) to deep red (0.75 – 1) are for positive correlations. Iteroparous and semelparous life histories are treated separately and we used two values of the population growth rate, $\lambda = 1.1$ and $\lambda = 3.0$. Here the noise, regardless of whether it is of blue, white or red colour, affects the first age group only.

their growth rates. Different combinations of density dependence and growth rates are known to yield very different population dynamics, e.g. stabilization processes, which seem to be the focus of the study of the paradigm of environmental forcing. This controversy certainly calls for a more detailed analysis.

To us it is obvious that, when the external noise modulates all age groups, the signature of the noise is far more

easily detectable as compared with cases where only one or a few age groups are affected. The Leslie matrix approach to modelling population dynamics addresses long-lived animals. To us it is less obvious that all age groups will be similarly vulnerable to external perturbation. We feel that the youngest age group(s) are those most severely affected by environmental stochasticity and that the effects of external perturbations diffuse through

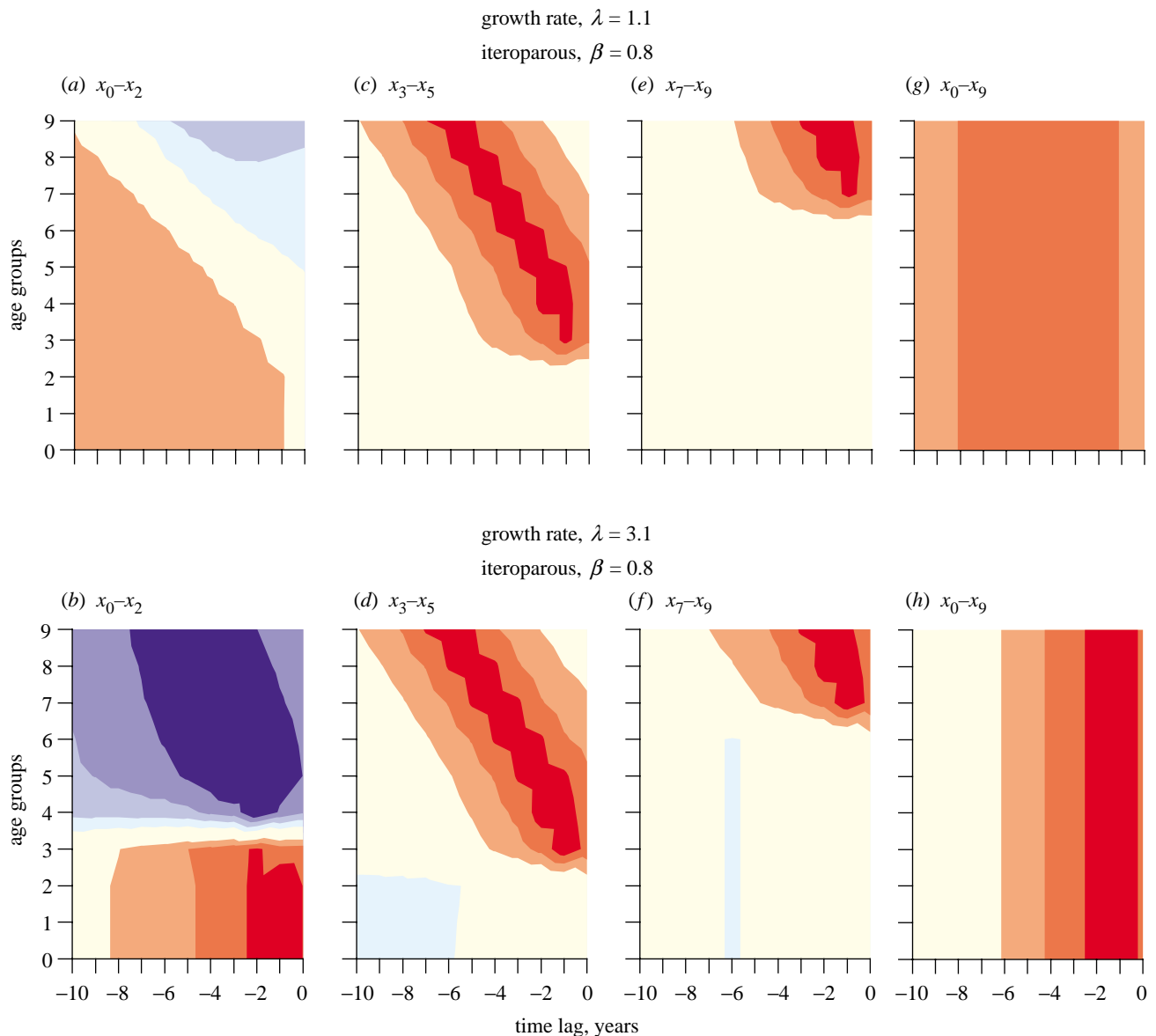


Figure 2. Age group- ($k = 10$) specific contour maps of the cross-correlation coefficients against various time-lags (from 0 to -10 years). The contour axis for the cross-correlation coefficient is the same as in figure 1. The colour of the noise is red ($\beta = 0.8$) and the data are exclusively for an iteroparous life history with two values of the population growth rate, $\lambda = 1.1$ and $\lambda = 3.0$. The age groups where the noise hits are indicated within each panel: (a,b) the three youngest age groups are vulnerable to the environmental stochasticity, (c,d) the noise-affected age groups are groups 3–5, (e,f) the three oldest age groups suffer from the noise, and (g,h) all age groups are similarly vulnerable to the environmental stochasticity.

the population age structure as the vulnerable cohort ages. Again, more research is needed in order to unravel the significance of the cohort effect and its influence on how visible the external noise can become in affecting the dynamics of age-structured populations.

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