Red environmental noise and the appearance of delayed density dependence in age-structured populations

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Previous work suggests that red environmental noise can lead to the spurious appearance of delayed density dependence (DDD) in unstructured populations regulated only by direct density dependence. We analysed the effect of noise reddening on the pattern of spurious DDD in several variants of the density-dependent age-structured population model. We found patterns of spurious DDD in structured populations with either density-dependent fertility or density-dependent survival of the first age class, inconsistent with predictions from unstructured population models. Moreover, we found that non-spurious negative DDD always emerges in populations with deterministic chaotic dynamics, regardless of population structure or the type of environmental noise. The effect of noise reddening in generating spurious DDD is often negligible in the chaotic region of population deterministic dynamics. Our findings suggest that differences in species' life histories may exhibit different patterns of spurious DDD (owing to noise reddening) than predicted by unstructured models.

Keywords: autocorrelation; delayed density dependence; age-structured models; red noise

1. INTRODUCTION

The abundances of natural populations are rarely constant over time, with many species exhibiting cyclic population dynamics (Kendall *et al.* 1998). This phenomenon has fascinated ecologists since the early twentieth century (Elton 1924), and, to this day, understanding its causal mechanisms has been one of the major research programmes in ecology (Andrewartha & Birch 1954; Lack 1954; Cappuccino & Price 1995; Turchin 2003). In recent years, the importance of delayed density dependence (hereafter DDD), that is, the delayed regulatory effects of past population densities on population growth rates, has been increasingly recognized in generating and maintaining population cycles (e.g. Turchin 1990; Turchin & Taylor 1992; Hoernfeldt 1994). DDD can, in principle, arise from a variety of biological mechanisms, such as trophic interactions (Royama 1992; Berryman & Turchin 1997) and delayed life-history effects, including within-generation cohort effects and among-generation maternal effects (see Beckerman *et al.* 2002 for review and references therein). The observation of DDD in many cyclic field populations has significantly improved our understanding of population regulation mechanisms.

Noise (variability) in environmental factors has long been known to play an important role in driving population cycles (e.g. Andrewartha & Birch 1954). Until recently, it has been generally assumed that environmental noise is white (random), and consequently much research has focused on the variance of noise (e.g. May 1973; Lande 1993). It has become increasingly clear, however, that physical environmental noise may often be red

(positively autocorrelated over time) (Mandelbrot & Wallis 1969; Steele 1985; Halley, 1996; Cuddington & Yodzis 1999). Some biotic factors may also act in the form of autocorrelated noise for organisms that are affected by them (Jiang & Shao 2003). Recent theoretical studies suggest that red noise leads to different risks of population extinction than white noise (Ripa & Lundberg 1996; Petchev *et al.* 1997; Cuddington & Yodzis 1999; Halley & Kunin 1999; Morales 1999; Ripa & Heino 1999; Heino *et al.* 2000; Heino & Sabadell 2003). Red noise also interacts with intrinsic density-dependent processes to affect population dynamics (Roughgarden 1975; Kaitala *et al.* 1997; Greenman & Benton 2003). For example, Kaitala *et al.* (1997) found that population dynamics tend to be more reddened when influenced by red than white noise. Greenman & Benton (2003) reported that red noise could interfere with deterministic unstable dynamics generated by density-dependent processes, causing irregular population cycles.

The effects of red environmental noise on population dynamics are also reflected by changes in the structure of density dependence. Several researchers have used simple unstructured models to show that populations experiencing only direct density dependence appear to be influenced by DDD, when subjected to red noise (Royama 1981; Ives 1995; Williams & Liebhold 1995; Jiang & Shao 2003). Furthermore, Jiang & Shao (2003) demonstrated that red noise may cause the appearance of either negative or positive DDD, depending on deterministic population dynamics. Such apparent DDD does not arise from intrinsic density-dependent processes alone, but from the interplay between noise and density dependence, and may therefore be perceived as spurious (Williams & Liebhold 1995, 1997; Berryman & Turchin 1997).

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The purpose of this article is to investigate the effects of noise reddening on the detection of spurious DDD in several simple age-structured matrix models. Previous studies on this topic have focused on unstructured models of homogenous populations (Royama 1981; Williams & Liebhold 1995; Jiang & Shao 2003), despite the fact that many organisms go through multiple stages during their life cycle or have spatially structured populations. We focus on age-structured populations here. The matrix models used in this paper, though still simple, incorporate the possibility that different population age classes may show differential responses to environmental variability, and provide some insights on how environmental noise, density dependence and population structure interact to affect population dynamics, particularly the occurrence of spurious DDD. As in previous studies, we restrict our attention to DDD from a population size two time periods earlier (i.e. second-order DDD), because it is the most important and the most commonly observed among DDD situations.

2. AGE-STRUCTURED POPULATION MODELS WITH NOISE

Our analyses of age-structured populations are based on density-dependent Leslie matrix models. For simplicity, we will restrict attention to models containing three age classes; the results for more age classes are qualitatively similar. The models take the form of

$$n_{t+1} = An_t, \quad (2.1)$$

where n_t is a column vector containing the population size of each age class at time t , and A is the Leslie projection matrix defined as

$$A = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{bmatrix}, \quad (2.2)$$

where F_i is the age-specific fertility, and P_i is the age-specific survival probability. We assume that population census takes place immediately after reproduction (i.e. $F_i = P_i m_i$, where m_i is the *per capita* reproductive output in age class i).

The undamped Leslie matrix model is biologically unrealistic, because it predicts exponential population growth (lacking any density dependence). Density dependence can be incorporated by making either fertility or survival probability, or both, a function of population density (Caswell 2001). We assume that density-dependent terms depend only on total population size, and choose a density-dependent term originally proposed by Hassell (1975),

$$g(N_t) = \frac{1}{(1 + N_t/K_t)^\beta}, \quad (2.3)$$

where N_t is the total population size of all age classes, K_t is a scaling factor affecting equilibrium population size, and β controls the strength of direct density dependence (under-compensation: $\beta < 1$; exact compensation: $\beta = 1$; over-compensation: $\beta > 1$).

We assume that environmental noise influences population size supported by the environment. In practice, this is achieved by including noise in K_t in equation (2.3). In each generation, K_t is given as

$$K_t = K_0 + \phi_t, \quad (2.4)$$

where K_0 is a constant, and the noise, ϕ_t , is drawn from a first-order autoregressive process

$$\phi_t = \alpha\phi_{t-1} + c(1 - \alpha^2)^{1/2}\varepsilon_t, \quad (2.5)$$

where α defines the strength of noise autocorrelation ($\alpha = 0$ for white noise, $0 < \alpha < 1$ for red noise), c is a constant controlling the amplitude of noise variation, and ε_t is standard normal variable (Ripa & Lundberg 1996).

We examined three simple density-dependent damping scenarios. For the first scenario, we suppose that density dependence affects the survival of all age classes ($P_{i,t} = g(N_t)P_i$); the second scenario assumes that density dependence affects the fertility of all age classes ($F_{i,t} = g(N_t)F_i$); the third scenario assumes the survival probability of only the newborn cohort being density dependent ($P_{1,t} = g(N_t)P_1$).

For each damping scenario, we varied the colour of environmental noise (white: $\alpha = 0$; moderately reddened: $\alpha = 0.4$; and strongly reddened: $\alpha = 0.8$), the strength of density dependence (under-compensation: $\beta = 0.5$; exact compensation: $\beta = 1$; and over-compensation: $\beta = 50$), and potential geometric growth rates (λ , the dominant eigenvalue of the undamped Leslie matrix), and iterated the density-dependent Leslie matrix model for 5000 time periods. We varied potential geometric growth rates by changing fertility but not survival rates. We discarded the data from the first 3000 time periods to remove transient dynamics, and used the remaining 2000 generations to score the lag 2 partial autocorrelation coefficient function (PACF[2]), the statistic commonly used to detect second-order DDD (Turchin 1990; Royama 1992). Spurious DDD was quantified by comparing the values of PACF[2] in red noise environments with white noise environments.

3. RESULTS

Two general patterns emerged, irrespective of the damping scenario. First, changes in growth rate have little effect on the characteristics of spurious DDD with under- or exact compensatory direct density dependence; i.e. when populations are characterized with deterministic monotonic damping behaviour, but have relatively large effects on the sign and strength of spurious DDD with over-compensatory direct density dependence; i.e. when deterministic population dynamics change from stable to unstable (figures 1 and 2). Second, increasing autocorrelation of the noise generally increases the strength of spurious DDD (figure 1).

(a) Scenario 1: density-dependent damping on the survival rate of all age classes

When the survival of each age class depends upon total population size, the resulting stable age distribution is identical to the stable age distribution of the undamped Leslie matrix model (Leslie 1948; Smouse & Weiss 1975). The results from the unstructured models (Jiang & Shao

Figure 1. Values of PACF[2] against λ , the potential geometric growth rate, for three different density-dependent damping scenarios with three different strengths of direct density dependence in a noisy environment. Scenario I: density-dependent survival in all age classes; scenario II: density-dependent fertility in all age classes; scenario III: density-dependent survival in the first age class only. All age classes in scenarios I and II share similar dynamics, whereas in scenario III the first age class has different dynamics from the other two age classes. Under-compensation: $\beta = 0.5$, exact-compensation: $\beta = 1$, over-compensation: $\beta = 50$. Noise with no autocorrelation: $\alpha = 0$ (filled circles); moderately autocorrelated noise: $\alpha = 0.4$ (open circles); and strongly autocorrelated noise: $\alpha = 0.8$ (filled triangles). The undamped Leslie matrix

$$A = \begin{bmatrix} F & 2F & 3F \\ 0.9 & 0 & 0 \\ 0 & 0.9 & 0 \end{bmatrix},$$

where F is varied to obtain the desired λ . $K_0 = 100$ in equation (2.4), $c = 20$ in equation (2.5). Choices of K_0 and c do not affect the results qualitatively.

Figure 2. Bifurcation diagrams for the first age class in over-compensatory populations ($\beta = 50$) with three different density-dependent damping scenarios. (a) Scenario I: density-dependent survival in all age classes; (b) scenario II: density-dependent fertility in all age classes; (c) scenario III: density-dependent survival in the first age class only. Parameter values as in figure 1.

2003) are recovered: under the influence of red noise, negative spurious DDD is observed for populations with monotonic damping deterministic behaviour, which includes populations regulated by under-compensatory and exact-compensatory direct density dependence (figure 1*a,b*), and populations characterized with over-compensatory direct

density dependence and very small growth rate (figures 1*c*, 2*a*). Positive spurious DDD is found in regions of oscillatory damping and limit cycles (figures 1*c*, 2*a*). Populations with deterministic chaos demonstrate negative DDD, even in the presence of white noise. Reddened noise leads to slightly negative spurious DDD (relative to white noise) in chaotic populations, but such DDD appears to be very small in magnitude, especially for noises with moderate autocorrelation (figure 1*c*).

(b) Scenario II: density-dependent damping on the fertility of all age classes

When only fertility is dependent on total population size, the resulting stable age distribution is different from that of the undamped Leslie matrix, with individuals more evenly distributed among age classes (Leslie 1948; Smouse & Weiss 1975), but the three age classes still exhibit similar dynamics. For populations regulated by under-compensatory direct density dependence, strongly reddened noise leads to slightly negative spurious DDD (relative to white noise) (figure 1*d*). By contrast, reddened noise leads to slightly positive spurious DDD in populations with exact-compensatory direct density dependence (figure 1*e*). For populations with over-compensatory direct density dependence, red noise leads to positive spurious DDD in the stable region (oscillatory damping), and slightly negative spurious DDD (relative to white noise) in regions of limit cycles and chaos (figures 1*f*, 2*b*). Spurious negative DDD due to noise reddening is of limited magnitude in the regions of limit cycles and chaos.

(c) Scenario III: density-dependent damping on the survival of the first age class

With density dependence affecting only the survival probability of the first age class, the first age class shows different dynamics than the second and third age classes. For populations regulated by under-compensatory direct density dependence, reddened noise leads to strongly negative spurious DDD in the first age class (figure 1*g*), and slightly negative spurious DDD in the second and third age classes (relative to white noise) (figure 1*j*). For populations regulated by exact-compensatory direct density dependence, reddened noise leads to strongly negative spurious DDD (relative to white noise) in the first age class (figure 1*h*), but virtually no spurious DDD is found for the second or third age class (figure 1*k*). Complex deterministic dynamics, including pseudo-periodicity and chaos, occupy much of the parameter space in populations with over-compensatory direct density dependence (figure 2*c*), and we observed no significant spurious DDD for any of the age classes, except for low values of growth rate (figure 1*i,l*).

4. DISCUSSION

In keeping with predictions from unstructured population models (Royama 1981; Williams & Leibhold 1995; Jiang & Shao 2003), our simulations demonstrate that both negative and positive spurious DDD could arise in age-structured populations subjected to red environmental noise. We have also demonstrated that different density-dependent scenarios can lead to qualitatively different

patterns of spurious DDD in age-structured populations. In unstructured population models, negative spurious DDD is associated with deterministic monotonic damping dynamics and positive spurious DDD is associated with deterministic oscillatory damping or limit cycles (Jiang & Shao 2003). We show that these simple predictions from unstructured models may not necessarily hold in structured models, even for the simple age-structured models explored here. For example, in age-structured populations with density-dependent fertility (scenario II), positive spurious DDD could arise in populations characterized by deterministic monotonic damping (figure 1e) and negative spurious DDD, albeit of small magnitude, could arise in populations characterized with limit cycles (figure 1f). In age-structured populations with density-dependent survival of the first age class (scenario III), different age classes exhibit different spurious DDD signature in populations with deterministic monotonic damping behaviour: strong negative spurious DDD is found for the first age class (figure 1g,h), and much weaker or negligible negative spurious DDD is found for the older age classes (figure 1j,k). These results suggest that, without detailed knowledge about how structured populations are affected by direct density dependence, it may be extremely difficult to predict spurious DDD associated with noise reddening, highlighting the need to take species life history into account when studying density dependence in red noise environments.

One of our notable findings is that, regardless of whether populations are structured or not, negative DDD is always found for populations in the chaotic region of deterministic dynamics, for both red and white environmental noises (figure 1c,f,i,l). Additional simulations indicate that negative DDD is always observed for chaotic populations even in the absence of environmental noise. These results also hold true for several other unstructured models that we explored, including models producing either blue (e.g. Ricker model: $N_{t+1} = N_t \exp[r(1 - N_t/K)]$) or red (e.g. Maynard Smith model: $N_{t+1} = rN_t/(1 + (N_t/K)^b)$) power spectra in the chaotic region (White *et al.* 1996). Thus, besides trophic interactions and delayed life-history effects, chaotic population dynamics may be another source of negative DDD. We note that chaotic dynamics have rarely been observed in natural populations, and if it is indeed rare, chaos may be a relatively unimportant contributor to negative DDD, as compared to trophic interactions or delayed life-history effects. However, the rarity of chaos in natural populations may well be due to the lack of appropriate statistical methods to detect chaos. With the development of more powerful analytical tools, evidence of chaos has begun to surface in both laboratory and field populations (Costantino *et al.* 1997; Perry *et al.* 2000; Turchin & Ellner 2000).

Another consistent observation, irrespective of population structure, is that the ability of noise reddening in generating spurious DDD is greatly diminished in the chaotic region of deterministic population dynamics (figure 1c,f,i,l). This finding is also independent of the underlying model structures (results not shown). Along the same line, Ranta *et al.* (2000) and Lundberg *et al.* (2002) reported that the impacts of environmental noise on population dynamics are largely invisible when

populations exhibit deterministic chaotic behaviour. Kaitala *et al.* (1997) also reported that the colour of population dynamics is insensitive to the colour of environmental noise in chaotic populations. These results suggest that certain characteristics of chaotic populations may be robust to environmental noise.

It has been suggested that, for age-structured populations, estimates of density dependence using autoregression techniques (e.g. PACF) may not directly correspond to the actual strength of density dependence, owing to interactions among age classes (Lande *et al.* 2002). This idea is clearly manifested in our simulations. For example, in populations with density-dependent fertility (scenario II) and under-compensatory direct density dependence, estimates of DDD take on positive rather than zero values with white noise (figure 1d). Focusing on spurious DDD due to noise reddening, we correct for this complication by always comparing the appearance of DDD in red noise environments with white noise environments.

Life-history characteristics also affect how other aspects of population dynamics respond to environmental noise. In investigating the visibility of environmental noise in age-structured populations, Kaitala & Ranta (2001) reported that environmental noise is largely invisible in semelparous populations and that red noise is more visible than white noise in iteroparous populations. Heino & Sabadell (2003) explored the effect of noise reddening on population extinction risk and found that red noise decreases the extinction risk of unstructured populations and increases the extinction risk of populations with more complex life histories.

In conclusion, we demonstrate that variation in density-dependent damping scenarios in age-structured population models can lead to different patterns of spurious DDD than predicted by unstructured populations in red noise environments. We note that only some of the simplest density-dependent age-structured models are explored here and some results may be contingent on our model assumptions. For example, semelparous populations, which are not studied here, may be likely to show differential spurious DDD patterns than iteroparous populations under the influence of red noise. Nevertheless, this study, as one of the first studies on how age-structured populations respond to reddened environmental noise (see also Mode & Jacobson 1987; Kaitala & Ranta 2001; Heino & Sabadell 2003), illustrates the importance of species life-history characteristics in affecting patterns of spurious DDD generated by the interaction between density dependence and coloured noise. Clearly, more research is needed to gain a more complete understanding of how environmental noise and life-history characteristics interact to affect population dynamics in a noisy environment. By contrast, the finding of spurious DDD in both structured and unstructured population models suggests that caution must be taken when interpreting sources of DDD observed in natural populations. It may be due solely to intrinsic density dependence; alternatively, it may be caused by the interaction between intrinsic density dependence and extrinsic autocorrelated noise.

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