Environmental Stochasticity

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Advanced article

Article Contents

Environmental stochasticity refers to unpredictable spatiotemporal fluctuation in environmental conditions. The term is often used in the literature on ecology and evolution. Unpredictability is defined as an inability to predict the future state precisely such that only its distribution can be known. The environment is typically defined as any set of abiotic (e.g. temperature and nutrient availability) and biotic (e.g. predator, competitor and food) conditions that organisms experience. Environmental stochasticity influences how population abundance fluctuates and affects the fate (e.g. persistence or extinction) of populations. In an evolutionary timescale, environmental stochasticity also affects the life history strategy of organisms. Environmental stochasticity is included in population models using univariate difference equations, stochastic matrix population models, stochastic differential equations and partial differential equations. Ecological data are analysed to determine the effect of environmental stochasticity using methods such as spectral analysis, capture–recapture analysis, state-space analysis, generalised linear models and multivariate statistical analyses.

Introduction

Environmental stochasticity refers to unpredictable spatiotemporal fluctuation in environmental conditions, affecting biological processes. Unpredictability is defined as an inability to predict the state precisely although its distribution may be known. The environment is typically defined as any set of abiotic conditions experienced by organisms, such as temperature, precipitation and nutrient availability. The environmental conditions fluctuate over time and space, which in turn directly or indirectly produce fluctuations in biological processes. These processes include growth/development, survival, reproduction, individual interactions and other biological processes. Consequently, environmental stochasticity is reflected in fluctuations in biological states such as the size or age distribution of individuals, population abundance, community structure and species distribution. The stochastic fluctuations in these biotic conditions are also considered environmental stochasticity from the point of view of the organisms that interact with the fluctuating biological states through competition, consumption/predation, mutualism, infection and other biological interactions.

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However, not all environmental fluctuations are stochastic (DeAngelis and Waterhouse, 1987). Fluctuation can be partitioned into stochastic and deterministic components (**Figure 1**). A deterministic process is one which, if understood precisely, enables future states to be predicted from current and past states. Daily and annual cycles are examples of predictable fluctuations, on which some stochastic components are often superimposed. Determining how much is deterministic or stochastic (thus predictable or unpredictable) precisely is often impossible. Therefore, it depends on our knowledge of the underlying processes and statistical properties of data. When our understanding of the system is limited, a large part of the fluctuation may be considered stochastic. Alternatively, models with both deterministic and stochastic components can be fitted to data to separate them through statistical model selection processes. Practicality is also a consideration; in some studies, complete knowledge of the underlying processes is not needed because only the distribution of states is of interest. In such cases, most or all of the mixed fluctuations may be attributed to environmental stochasticity, but it is important to recognise that observed fluctuations involve both deterministic and stochastic components.

Other causes of fluctuations in ecological systems include density-dependent process producing nonlinear dynamics (**see also: Nonlinear Dynamics and Chaos**) and species interactions such as predator–prey interactions (**see also: Predation on Animals**). Ecological and evolutionary processes are also affected by demographic stochasticity (Lande *et al.*, 2003), and ecological data are affected by observational errors. Separating these

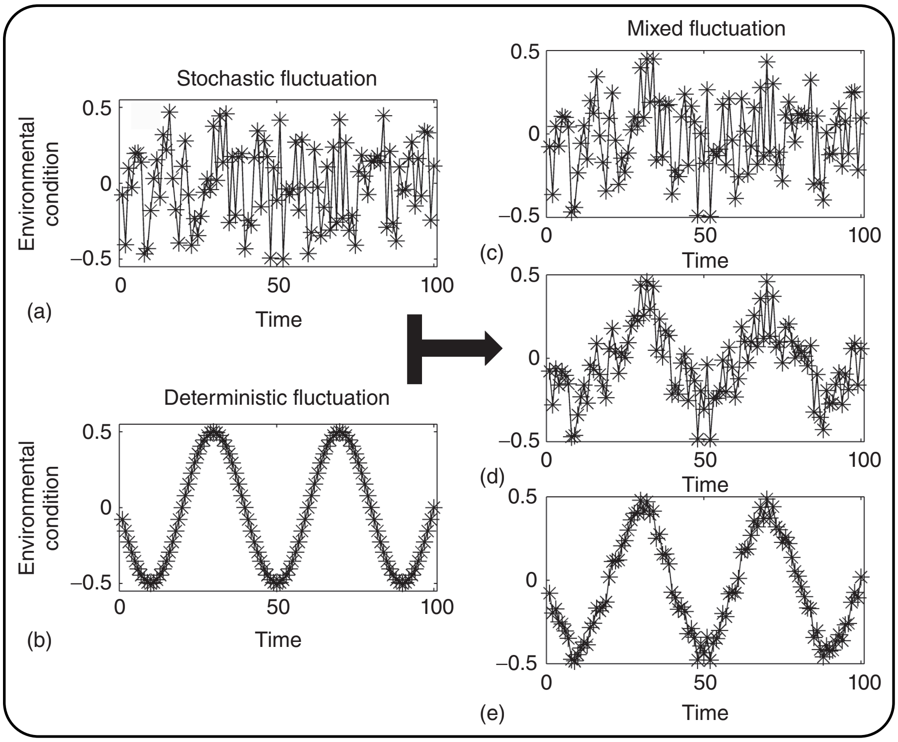

Figure 1 Stochastic and deterministic fluctuations: (a) purely stochastic fluctuation, (b) purely deterministic fluctuation, (c) mixture with high stochasticity, (d) mixture with intermediate stochasticity and (e) mixture low stochasticity.

processes is a challenging part of ecological and evolutionary research.

In the remainder of this article, characteristics of environmental fluctuation and potential effects on ecological and evolutionary systems are described. Then, mathematical models and statistical methods for the analysis of environmental stochasticity in ecology and evolutionary demography are briefly summarised.

Characteristics of Environmental Fluctuation

Many environmental variables exhibit a mixture of stochastic and deterministic variations. This often becomes clearer as more data points are included in a time series (Halley, 1996). Historical records suggest that both marine and terrestrial environmental conditions tend to exhibit smooth variation (cyclic deterministic pattern) on timescales longer than approximately 50 years. However, over shorter timescales, environmental conditions appear to be more stochastic. Marine environmental conditions tend to be less stochastic than those in the terrestrial environment (Steele, 1985). For example, ocean temperature in the North Pacific exhibits a decadal oscillation (Mantua and Hare, 2002), and this is thought to be one of the main causes of fluctuations in salmon and other fish populations in the North Pacific. Furthermore, Vasseur and Yodzis (2004) showed that terrestrial environmental variables tend to include a greater stochastic component, increasing with the distance from coastal areas. This is thought to result from the decoupling of marine and terrestrial environmental systems over short timescales due to differences in heat capacity between air and water. The greater heat capacity of water causes the temperature of marine systems to fluctuate slowly, producing a smooth pattern in environmental fluctuation.

Effects on Ecological Systems

Effects on population dynamics

Stochastic fluctuations in environmental conditions cause stochastic fluctuations in population processes (survival, fecundity, growth and development), which, in turn, cause fluctuations in population states (e.g. abundance, age/stage distribution and the total reproductive potential of a population). Such fluctuations increase the uncertainties in the forecasts of future population states as well as our understanding of the systems. These uncertainties often require us to take precautionary measures in the harvests of exploited species as well as the conservation of protected species (Garcia, 1994). Furthermore, stochastic fluctuations in survival and reproductive rates due to environmental stochasticity reduce long-run population growth rate (Lande *et al.*, 2003). However, it has been shown that environmental stochasticity can also increase a long-run population growth rate if it affects growth or development of individuals (Doak *et al.*, 2005).

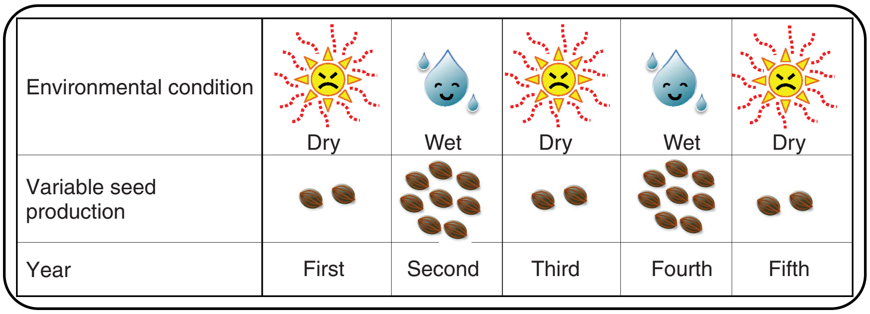

Figure 2 Diagram depicting the sequence of 'dry' and 'wet' conditions and the number of viable seeds produced under the corresponding environmental condition.

Effects on small populations and population extinction

For populations with small numbers of individuals, the chance of occurrence of consecutive periods of unfavourable environmental conditions due to environmental stochasticity can drive a population to extinction. This concept is incorporated in a population viability analysis (PVA; Boyce, 1992; Beissinger and McCullough, 2002). In one of the simplest PVA, termed count-based PVA, environmental stochasticity is assumed to be the only source of fluctuation in population abundance, and the probability of the population reaching a certain critical threshold level, termed quasi-extinction threshold, is calculated using a diffusion model (Morris and Doak, 2002). However, this approach has been criticised on the basis of the difficulty in accurately estimating model parameters (Ellner and Holmes, 2008). **See also: Conservation of Populations and Species**

Spatial synchronisation and environmental stochasticity

Environmental stochasticity can also produce synchronisation in population dynamics over space. In ecology, this effect is termed the Moran effect (Moran, 1953). Before the discovery of the Moran effect, the causes of fluctuation and synchronisation in population density were considered to be the same: for example, a large-scale environmental fluctuation causing synchronised fluctuation over space. However, the Moran effect suggests the causes of fluctuation and synchronisation can be different. For example, periodic dynamics caused by predator–prey interaction at two separate locations can be synchronised by a small amount of individual exchanges. This synchronisation can also occur without any exchange of individuals if there is a small amount of correlated environmental stochasticity affecting the systems at both places.

Effects on Evolutionary Processes

Environmental stochasticity also plays an important role in the evolution of life history strategies by affecting the fitness of organisms. For example, the fluctuation leads to the variation in the number of offspring, and this variation reduces the geometric mean of offspring produced over time, which is commonly used to predict the long-term outcome of evolution (**see also: Fitness**). Suppose that there are two types of years, *wet* and *dry*, occurring with equal probability, and the annual numbers of offspring produced are eight and two (the average is five) in wet and dry years, respectively (**Figure 2**). If those years come alternatively, a grandmother has 8×2 grandchildren after 2 years and the geometric mean is a square root of 16 (i.e. 4), which is the Darwinian fitness over one generation. It is less than 5, which is the geometric mean of 5×5 when the average number of offspring is produced every year without any variation over time (Philippi and Seger, 1989). In response, organisms have developed strategies to minimise the fitness reduction in the course of evolution (Gillespie, 1974) by diversifying the risk.

Suppose that there are two types of years, A and B, occurring with equal probability. A plant species reproduces two types of seeds, type 1 and 2, and the sum of the numbers is 12. Type 1 is more adaptive for year A than year B, say the survival probability is 2/3 in year A and is 1/2 in year B. On the other hand, type 2 is completely reversed. If the plant reproduces only type 1, the expected numbers of seeds in years A and B are $12 \times (2/3) = 8$ and $12 \times (1/3) = 4$, respectively. However, if the plant produces six type 1 and six type 2 seeds at the same time, the expected number of seeds is always $6 \times (2/3) + 6 \times (1/3) = 6$. Therefore, the strategy to reproduce both types of seeds gains a larger number (geometric mean is $\sqrt{6 \times 6} = 6$) than the strategy of reproducing only type 2 seeds (the geometric mean is $\sqrt{4 \times 8} = 4\sqrt{2}$) despite the number of seeds produced being the same. The way to reduce the variation in yearly fitness using multiple types of seeds is called germination heteromorphism, and it has been reported by several botanists (Silvertown, 1984). This concept of diversification of risk is in an old saying, 'don't put all your eggs in one basket', and this type of strategy is generally called a bet-hedging strategy. **See also: Life History Theory; Reproductive Strategies**

Calculating the geometric mean fitness can be complicated if variations in the types of environment and/or responses of organisms are high. It can be estimated using the geometric mean from time 0 and t of population growth rate:

$$\sqrt[t]{\prod_{k=0}^{t-1} r_k} = \sqrt[t]{\frac{N_t}{N_0}} \qquad (1)$$

where N_t and r_t represent population size and the population growth rate at time t, respectively (see the section titled 'Stochastic Discrete-time Models' for the detail). When t approaches infinity, that is long-term time average, it is called 'stochastic population growth rate' (λ_s) (Cohen, 1977a; Tuljapurkar and Orzack, 1980; Caswell, 2001). The evolution of life history strategies in a fluctuating environment can be understood by comparing λ_s (Horvitz *et al*., 2005). The strategy with the highest λ_s is the optimal strategy in a fluctuating environment.

Optimal strategies are also influenced by deterministic components of environmental fluctuation. For example, most organisms are adapted to cope with daily and/or annual environmental fluctuations. However, the relative importance of deterministic and stochastic components on life history evolution is uncertain (Orzack and Tuljapurkar, 2001). This uncertainty results partially from the challenges in its empirical determination. First, it is difficult to determine the amount of environmental fluctuation that is stochastic (unpredictable) for the organisms of interest, as it can be different from the stochasticity that is perceived by human observers. Second, environmental fluctuation differs depending on the spatiotemporal scale of the environment that affects organisms. For example, long-lived organisms are buffered against short-term fluctuations, so high-frequency fluctuations appear to be irrelevant to their life history evolution. However, it may be that such organisms evolved to have a long life span in response to the short-term environmental fluctuations. Thus, from an evolutionary standpoint, short-term fluctuations are an important factor determining the life history strategy.

Mathematical Models

There are four basic models to describe the population dynamics under stochastic environment, depending on the presence of inner structure within populations and the discreteness of time. The discrete-time model without inner structure is described using a difference equation with respect to population size, that is a stochastic discrete-time model. The continuous-time model without inner structure is an application of a stochastic differential equation (SDE). The discrete-time model with population structure is a stochastic matrix population model. The continuous-time model of a structured population is an application of partial differential equation (PDE). These models are described briefly.

Stochastic discrete-time models

A stochastic discrete-time model for geometrically growing unstructured populations is called the Lewontin–Cohen model (Lewontin and Cohen, 1969), and it takes the form of a simple difference equation with stochastically fluctuating per capita population growth rate. Suppose that the population size increases by a rate r_t at each time step:

$$N_{t+1} = r_t N_t \tag{2}$$

where N_t is the population size at time t and r_t gives the population growth rate between time t and $t+1$. Equation (2) is the simplest difference equation with stochasticity when we assume the per capita population growth rate is independent of the population size but depends on environmental conditions. Environmental stochasticity affects the per capita population growth rate so that population size also fluctuates stochastically. Assuming that the population size at time 0 is N_0, then eqn (2) is solved as follows:

$$N_t = N_0 \prod_{k=0}^{t-1} r_k \tag{3}$$

By obtaining the natural logarithm of both sides of eqn (3) and by applying algebraic manipulations, we obtain

$$\log\left(\frac{N_t}{N_0}\right) = \sum_{k=0}^{t-1} \log r_k \tag{4}$$

The trajectories of $\log(N_t/N_0)$ are drawn in **Figure 3**, starting from a unique initial value, N_0. Each trajectory fluctuates at every time step due to environmental fluctuation and the width of the variation increases with time. If r_t exhibits white noise fluctuation, then the following relationship is derived by applying the central limit theorem:

$$\log\left(\frac{N_t}{N_0}\right) \sim \text{Normal}(t \log \lambda_s, t\sigma^2) \tag{5}$$

where $\log \lambda_s$ and σ^2 are the mean and variance of $\log(r_t)$ (Cohen, 1977b; Tuljapurkar and Orzack, 1980). In other words, the natural log of relative population size at time t is normally distributed with mean $t \log \lambda_s$ and variance $t\sigma^2$. Therefore, the mean and variance increase linearly with time t (**Figure 3**). It should be noted that neither r_t nor $\log(r_t)$ needs to be normally distributed for eqn (5) to be valid asymptotically.

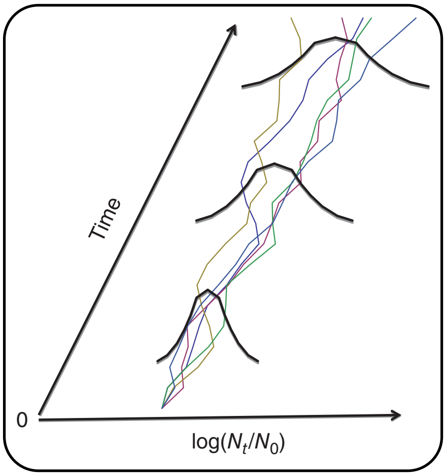

Figure 3 Sample paths of logarithm of population size. Each solid line represents the sample path starting from the unique initial value. The thick lines are the normal distribution with mean $t\log\lambda_s$ and variance $t\sigma^2$. The distribution expands with time.

Stochastic matrix population models

Stochastic matrix population models are discrete-time models for stage-structured populations. In deterministic matrix population models, life history parameters (survival rates, reproductive rates and the rates of transitions among stages) are incorporated into a projection matrix (**see also: Discrete Analysis (Matrix Models)**). The $<i,j>$ element of a projection matrix $\mathbf{A}_t$ is the per capita rate of contribution of stage *j* to stage *i*. Typically, the first row is for reproduction; therefore, the first row of the *j*th column is the fertility rate of individuals in stage *j*. Other parameters are the transition rates of individuals from stage *j* to stage *i* between time *t* and $t+1$. This matrix is used to project a vector of stage-specific abundance as

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t \tag{6}$$

where $\mathbf{n}_t$ is a vector whose components are the abundance of individuals in different stages. In the deterministic model, $\mathbf{A}_t = \mathbf{A}_{t+1}$. In order to incorporate environmental stochasticity in the model, the elements of the projection matrix $\mathbf{A}_t$ are stochastically varied over time. Once the projection matrices are determined, associated statistics can be calculated, including asymptotic population growth rate, stable stage distribution, and their sensitivities to changes in the mean and variance of population parameters (Tuljapurkar, 1982; Tuljapurkar *et al*., 2003).

Stochastic population growth rate (λ_s) in stochastic matrix population models is calculated using the limit of the geometric mean over *t* years, similarly to eqn (1) in the section titled 'Effects on Evolutionary Processes', as

$$\log \lambda_s = \lim_{t\to\infty} \frac{1}{t} \log \frac{N_t}{N_0} = \lim_{t\to\infty} \frac{1}{t} \log \left\{ \frac{\|\mathbf{A}_{t-1}\mathbf{A}_{t-2} \cdots \mathbf{A}_0 \mathbf{n}_0\|}{\|\mathbf{n}_0\|} \right\} \tag{7}$$

where $\|\mathbf{x}\|$ is the element-sum of a vector $\mathbf{x}$ (Tuljapurkar and Orzack, 1980; Heyde and Cohen, 1985). In conservation biology and evolutionary demography, it is used to evaluate whether the long-term growth rate of a population in question exceeds 1 or not and allows us to examine the effect of fluctuating environment on the population dynamics. A formula for calculating λ_s and its sensitivity to the mean and variance of vital rates when the environmental stochasticity is serially autocorrelated can be found in Tuljapurkar and Haridas (2006).

Stochastic differential equation (SDE) models

SDE adds stochasticity in an ordinary differential equation (Higham, 2001). For example, the exponential growth model is given as

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t) \tag{8}$$

where *r* and $N(t)$ represents the intrinsic growth rate of population and the population size at time *t*. This is the simplest and most famous model in mathematical biology termed the Malthusian equation. If *r* is affected by a stochastically fluctuating environment, then eqn (8) becomes

$$\mathrm{d}N(t) = rN\mathrm{d}t + \sigma N \mathrm{d}B \tag{9}$$

where d*B* is an *iid* stochastic term with mean 0 and variance 1, that is white noise fluctuation. The second term of the right-hand side of eqn (9) represents the stochastic term, the so-called Brownian motion. SDEs, such as eqn (9), can be calculated using one of two methods: Ito or Stratonovich integral (Higham, 2001). With the Stratonovich integral, the natural log of $N(t)/N(0)$ is normally distributed with the mean *tr* and variance $t\sigma^2$ (Øksendal, 2013). Note that *r* is equivalent to log λ_s in the Lewontin–Cohen model.

A system of SDEs can be used to model more complex biological processes. For simple linear situations, the solutions to the SDE models can be found analytically using a transfer function method (Nisbet and Gurney, 1982). However, simulations are often required when equations are nonlinear. Simulation of SDE models requires great care because it is possible to derive different solutions depending how the integrals are calculated (Higham, 2001).

Partial differential equation models

PDE is a differential equation with multiple independent variables and contains partial derivatives with respect to them. It is closely related to the above two models: SDEs and stochastic matrix population models. When a population is structured by 'size' of individuals such as biomass, folk length and diameter at breast height (DBH), then the independent variable that structures a population is continuous (as opposed to finite discrete categories). PDE models handle it by including the structural parameter as another independent variable. Suppose $P(x, t)$ denotes a density distribution of size *x* at time *t*, the dynamics are described as follows:

$$\frac{\partial P(x,t)}{\partial t} = -\frac{\partial G(x)P(x,t)}{\partial x} - M(x)P(x,t) \tag{10}$$

where $G(x)$ and $M(x)$ are growth rate and mortality rates of individuals with size *x*, respectively. This equation is known as the Von Foerster equation (Sinko and Streifer, 1967; de Roos, 1997). If the growth rate, $G(x)$, varies because of fluctuating environment, the dynamics equation is a second-order PDE, adding a diffusion term to eqn (10):

$$\frac{\partial P(x,t)}{\partial t} = \frac{1}{2}\frac{\partial^2 D(x)P(x,t)}{\partial x^2} - \frac{\partial \overline{G}(x)P(x,t)}{\partial x} - M(x)P(x,t) \tag{11}$$

where $\overline{G}(x)$ and $D(x)$ are the first and the second moments of $G(x)$, respectively. When we assume zero-mortality rate, this equation is generally known to have the same form as the forward Kolmogorov diffusion equation or Fokker–Planck equation (Goel and Richter-Dyn, 2016). If $G(x)$ has white noise fluctuation around the mean *gx* with the variance $\sigma^2 x^2$, then $\overline{G}(x) = [g + (\sigma^2/2)]x$ and $D(x) = \sigma^2 x^2$. The solution, $P(x, t)$, of eqn (11) is generally difficult to obtain analytically and the numerical solution is calculated using the appropriate discretisation along independent variables. The numerical calculation again requires a great care for discretisation, that is the increments of time (Δt) and size (Δx). Equation (11) can be viewed as the size-continuous version of matrix population models. The relationship between matrix population models and PDEs are discussed explicitly in Takada and Hara (1994).

Statistical Analysis

Statistical methods for the analysis of population data affected by environmental stochasticity can be classified into five general categories: (1) conducting spectral analysis and fitting autoregressive moving average (ARMA) models, (2) fitting state-space models, (3) capture–recapture analysis, (4) regressions and related analyses and (5) multivariate statistical analysis. These approaches are briefly outlined and references are provided.

Spectral analysis and fitting autoregressive moving average (ARMA) model

When long time series are available, a periodogram, correlogram and partial autocorrelogram can be plotted (Diggle, 1990). A periodogram is a plot of relative importance (vertical axis) of different frequencies (horizontal axis) in a time series, and it tells us what frequencies are represented in the data. A correlogram shows the correlation (vertical axis) between time series and its own time-lagged values plotted against the amount of the time-lag. Finally, a partial autocorrelogram is similar to the correlogram except that it controls for the correlation at shorter time-lags. These three types of figures can be used for characterising the statistical properties of time series, and the analysis is called spectral analysis.

Once the spectral analysis is done, an ARMA model can be fitted to data (Diggle, 1990). ARMA models are continuous-state discrete-time models in which a state at time t is expressed in terms of the past states and the stochastic component of the fluctuation:

$$X_t = \sum_{k=1}^{p} a_{t-k} X_{t-k} + Z_t + \sum_{k=1}^{q} b_k Z_{t-k} \tag{12}$$

where X_t is the state (which may be an environmental state, or an ecological state such as population abundance) at time t, Z_t is an *iid* random variable with mean zero and finite variance, and the integer values p and q are the orders of autoregressive and moving average processes of the model, respectively. These orders can be determined based on the results of the spectral analysis. ARMA models together with spectral analyses are particularly useful when trying to statistically characterise stochastic fluctuation in time series data when the underlying processes are not well known. Once fitted to the data, the ARMA model can be used for simulating time series that have the same statistical characteristics as the original data or for predicting future states.

State-space model

State-space models (Harvey, 1989) are statistical models that include a deterministic process, a stochastic process (i.e. process error) and stochastic observational errors. By fitting the model to time series data, it allows us to partition the fluctuations in the data into those three components (Dennis *et al*., 2006). This approach is used in ecological studies to analyse time series, such as counts of individuals, catch per unit effort and transect data. It has been applied to fishery data (Schnute, 1994) as well as data from protected species as a part of PVA (Lindley, 2003). Recently, combining ARMA and state-space models, a vector autoregressive state-space method was developed. This model, for example can incorporate species interactions under environmental stochasticity (Ives *et al*., 2003).

Capture–recapture analysis

Capture–recapture analysis estimates the survival rate from individual capture histories (Lebreton *et al*., 1992), and it can be used for estimating the effect of environmental stochasticity on vital rates. There are two basic approaches. If the observation of a stochastically fluctuating environmental condition is available, then it can be incorporated into the model as a covariate. Alternatively, survival rate can be estimated for each time step, and variation in the mean estimates can be attributed to the effect of environmental stochasticity. The advantage of capture–recapture analysis is that, by default, it separates observational errors in the estimations and that they estimate survival rates directly rather than inferring them from changes in population density.

Regression models and related methods

Generalised linear models (McCullagh and Nelder, 1989) and related regression methods are the most common approaches to analyse the time series data in ecology. The method requires observation of the dependent variable (e.g. count of individuals) and independent variables (e.g. fluctuating environmental conditions), and their associations are determined statistically. Practically, it assumes that a large part of the environmental stochasticity, if any, can be explained by the independent variables. Although it is simple, it suffers from two major problems: colinearity among variables (Knape and de Valpine, 2011) and nonstationarity of the time series (Bence, 1995, Pyper and Peterman, 1998; Zhou *et al*., 2016), both of which can cause spurious statistical inference. To overcome these issues, partial least squares regression for overcoming colinearity (Garthwaite, 1994) and cointegration for overcoming nonstationarity (Engle and Granger, 1987) can be applied.

Multivariate statistical analysis

When multiple population data and multiple environmental data are collected, multivariate statistical analyses can be applied. For example, various factor analyses (Manly, 2005) are applied to population data and environmental data, and statistical association between them can be analysed. An advantage of this approach is that, when short but many time series are available, underlying patterns in the data can be found using multivariate statistical analysis (Fujiwara and Mohr, 2009). However, the patterns found under multivariate statistical methods may or may not be relevant biological processes. Consequently, this type of analyses tends to be explorative.

References

Beissinger SR and McCullough DR (2002) *Population Viability Analysis*. Chicago, IL: The University of Chicago Press.

Bence JR (1995) Analysis of short-time series – correcting for autocorrelation. *Ecology* **76**: 628–639.

Boyce MS (1992) Population viability analysis. *Annual Review of Ecology and Systematics* **23**: 481–506.

Caswell H (2001) *Matrix Population Models*. Sunderland, MA: John Wiley & Sons, Ltd.

Cohen JE (1977a) Ergodicity of age structure in populations with Markovian vital rates. II. General states. *Advances in Applied Probability* **9** (1): 18–37.

Cohen JE (1977b) Ergodicity of age structure in populations with Markovian vital rates, III: finite-state moments and growth rate; an illustration. *Advances in Applied Probability* **9** (3): 462–475.

DeAngelis DL and Waterhouse JC (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* **57**: 1–21.

Dennis B, Ponciano JM, Lele SR, Taper ML and Staples DF (2006) Estimating density dependence, process noise, and observation error. *Ecological Monographs* **76**: 323–341.

de Roos AM (1997) A gentle introduction to physiologically structured population models. In: Tuljapurkar S and Caswell H (eds) *Structured-population Models in Marine, Terrestrial, and Freshwater Systems*, pp. 119–204. New York, NY: Chapman & Hall.

Diggle PJ (1990) *Time Series: A Biostatistical Introduction*. Oxford, UK: Oxford Science Publications.

Doak DF, Morris WF, Pfister C, Kendall BE and Bruna EM (2005) Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**: E14–E21.

Ellner SP and Holmes EE (2008) Commentary on holmes et al. (2007): resolving the debate on when extinction risk is predictable. *Ecology Letters* **11**: E1–E5.

Engle RF and Granger CWJ (1987) Cointegration and error correction – representation, estimation, and testing. *Econometrica* **55**: 251–276.

Fujiwara M and Mohr MS (2009) Identifying environmental signals from population abundance data using multivariate time-series analysis. *Oikos* **118**: 1712–1720.

Garcia SM (1994) The precautionary principle: its implications in capture fisheries management. *Ocean & Coastal Management* **22**: 99–125.

Garthwaite PH (1994) An interpretation of partial least-squares. *Journal of the American Statistical Association* **89**: 122–127.

Gillespie JH (1974) Natural selection for within-generation variance in offspring number. *Genetics* **76**: 601–606.

Goel NS and Richter-Dyn N (2016) *Stochastic Models in Biology*. London, UK: Academic Press.

Halley JM (1996) Ecology, evolution and 1/f-noise. *Trends in Ecology & Evolution* **11**: 33–37.

Harvey AC (1989) *Forecasting, Structural Time Series Models and the Kalman Filter*. Cambridge, UK: Cambridge University Press.

Heyde CC and Cohen JE (1985) Confidence-intervals for demographic projections based on products of random matrices. *Theoretical Population Biology* **27**: 120–153.

Higham DJ (2001) An algorithmic introduction to numerical simulation of stochastic differential equations. *SIAM Review* **43**: 525–546.

Horvitz CC, Tuljapurkar S and Pascarella JB (2005) Plant–animal interactions in random environments: habitat stage elasticity, seed predators, and hurricanes. *Ecology* **86**: 3312–3322.

Ives AR, Dennis B, Cottingham KL and Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* **73**: 301–330.

Knape J and de Valpine P (2011) Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society B* **278**: 985–992.

Lande R, Engen S and Saether BE (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford, UK: Oxford University Press.

Lebreton JD, Burnham KP, Clobert J and Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals – a unified approach with case studies. *Ecological Monographs* **62**: 67–118.

Lewontin RC and Cohen D (1969) On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences* **62**: 1056–1060.

Lindley ST (2003) Estimation of population growth and extinction parameters from noisy data. *Ecological Applications* **13**: 806–813.

Manly BFJ (2005) *Multivariate Statistical Methods: A Primer*, 3rd edn. Boca Raton, FL: Chapman and Hall/CRC.

Mantua NJ and Hare SR (2002) The pacific decadal oscillation. *Journal of Oceanography* **58**: 35–44.

McCullagh P and Nelder JA (1989) *Generalized Linear Models*, 2nd edn. Boca Raton, FL: Chapman & Hall/CRC.

Moran PAP (1953) The statistical analysis of the Canadian lynx cycle. 2. Synchronization and meteorology. *Australian Journal of Zoology* **1**: 291–298.

Morris WF and Doak DF (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates.

Nisbet RM and Gurney W (1982) *Modelling Fluctuating Populations*. Caldwell, NJ: The Blackburn Press.

Øksendal B (2013) *Stochastic Differential Equations: An Introduction with Applications*. Heidelberg: Springer-Verlag.

Orzack SH and Tuljapurkar S (2001) Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology* **82**: 2659–2665.

Philippi T and Seger J (1989) Hedging one's evolutionary bets, revisited. *Trends in Ecology & Evolution* **42**: 41–44.

Pyper BJ and Peterman RM (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data (vol 55, pg 2127, 1998). *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 2710.

Schnute JT (1994) A general framework for developing sequential fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 1676–1688.

Sinko JW and Streifer W (1967) A new model for age-size structure of a population. *Ecology* **48**: 910–918.

Silvertown J (1984) *Introduction to Plant Ecology*. New York, NY: Longman.

Steele JH (1985) A comparison of terrestrial and marine ecological systems. *Nature* **313**: 355–358.

Takada T and Hara T (1994) The relationship between the transition matrix model and the diffusion model. *Journal of Mathematical Biology* **32**: 789–807.

Tuljapurkar S and Orzack SH (1980) Population-dynamics in variable environments. 1. Long-run growth-rates and extinction. *Theoretical Population Biology* **18**: 314–342.

Tuljapurkar SD (1982) Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* **21** (1): 114–140.

Tuljapurkar S, Horvitz CC and Pascarella JB (2003) The many growth rates and elasticities of populations in random environments. *American Naturalist* **162** (4): 489–502.

Tuljapurkar S and Haridas CV (2006) Temporal autocorrelation and stochastic population growth. *Ecology Letters* **9**: 327–337.
Vasseur DA and Yodzis P (2004) The color of environmental noise. *Ecology* **85**: 1146–1152.
Zhou C, Fujiwara M and Grant WE (2016) Finding regulation among seemingly unregulated populations: a practical framework for analyzing multivariate population time series for their interactions. *Environmental and Ecological Statistics* **23**: 181–204.

Further Reading

Caswell H (2001) *Matrix Population Models*. Sunderland, MA: John Wiley & Sons, Ltd..
Nisbet RM and Gurney W (1982) *Modelling Fluctuating Populations*. Caldwell, NJ: The Blackburn Press.