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Stochasticity in the extinction process

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1. Fedrowitz, K. 2008. Epiphyte metacommunity dynamics.
2. Johansson, V. 2008. Metapopulation dynamics of epiphytes in a landscape of dynamic patches.
3. Ruete, A. 2008. Beech epiphyte persistence under a climate change scenario: a metapopulation approach.
4. Schneider, N. 2008. Effects of climate change on avian life history and fitness.
5. Berglund, Linnea. 2008. The effect of nitrogen on the decomposition system.
6. Lundström, Johanna. 2008. Biodiversity in young versus old forest.
7. Hansson, Karna. 2008. Soil Carbon Sequestration in Pine, Spruce and Birch stands.
8. Jonasson, Dennis. 2009. Farming system transitions, biodiversity change and ecosystem services.
9. Locke, Barbara. 2010. Sustainable Tolerance of Varroa destructor by the European honey bee Apis mellifera.
10. Kärvemo, Simon. 2010. Population dynamics of tree-killing bark beetles – a comparison of the European spruce bark beetle and the North American mountain pine beetle.
11. Jeppsson, Tobias. 2009. Stochasticity in the extinction process.

Contents

Introduction

What is typical for ecology and ecological systems? To me, one of the first things that spring to mind is complexity and variation. These topics have long been acknowledged in ecology, and have been targeted as two of the reasons why it is notoriously hard to produce universal general theory in ecology (Lawton, 1999; Belovsky et al, 2004). Lawton (1999) pinpointed complexity within and variation between communities, together producing numerous contingencies for each law-like statement, as the main reason that generalities are hard to come by in community ecology. In population biology Pimm & Redfearn (1988) studied series of population censuses longer than 50 years, and came to the conclusion that variability increased continuously with time. Variation in ecological systems arise on many levels, ranging from large scale environmental fluctuations acting over hundreds or thousands of years, to small scale variations in individual foraging efficiency. In between of these extremes we find, for instance, spatial and temporal variation in environmental conditions in a landscape, differences in performance between individuals, which can stem both from genetic or environmental causes, and variation between sexes in survival rates. The two characteristics I have mentioned, complexity and variation, make it notoriously hard to fully understand and accurately predict how ecological systems will develop over time.

In any model, conceptual or mathematical, we set boundaries to the system under study, and thereby choose what to include explicitly in the model and what to treat as external environment (Olsson & Sjöstedt, 2004). Therefore, the external environment and its influences can include anything from abiotic fluctuations to biotic factors such as predators or ecosystem processes. Under this view, environmental variation can be seen as the aggregated influence from multiple paths, for which the detailed workings are mostly unclear. Since we often lack in knowledge on the causes of much ecological variation, this also introduces randomness into our systems. Even if we have good information on the range, correlation structure and time scale of the variation, we still cannot predict exactly how the environment will change over time. Therefore probabilistic statements are often necessary, and this transcends into our population and ecosystem models. Since much of Conservational Biology deals with small populations, the randomness due to the discreteness of population numbers must also be included in population models (May, 1973; Shaffer, 1981), and this introduce another source of variation.

The need for stochastic models in population dynamics was recognised in the late 60's (Lewontin & Cohen, 1969; May, 1973; Soulé & Wilcox, 1980), and it has developed as being an essential part of Population Viability Analysis (PVA), where the prospects of future survival of populations are evaluated (Boyce, 1992; Beissinger & Westphal, 1998; Beissinger & McCullough, 2002). The use of stochastic models has been questioned by Caughley (1994) and Ludwig (1999), and these authors claim that too much focus on aspects important for small and fragmented populations can detract from the often deterministic reasons for population declines. The following discussion filled the middle ground between these opposing viewpoints, and acknowledges that both the small population paradigm and the declining population paradigm should contribute to conservation efforts (Hedrick et al., 1996; Boyce, 2002).

In this essay I will focus on the theoretical framework for handling complexity and variation in single population dynamics, and more specifically on how this variation affects the probability of population extinction. The scale of variation in the following pages will deal with populations and species, in contrast to ecosystems and species communities. I will cover definitions of environmental and demographic stochasticity; give a brief overview of techniques used for modelling stochasticity; and review the general results that have been

obtained. I will also touch upon methods on how to measure variation. Finally, I will mention other aspects of stochastic models not treated here, and discuss the problems and possibilities of stochastic population dynamics in conservation ecology.

Sources of random variation

As touched on in the introduction there exist many factors that introduce randomness in population models. I will now define and discuss the two main components; environmental and demographic stochasticity.

Environmental stochasticity

The most obvious form of variation that individuals are exposed to is temporal fluctuations in their living environment (temporal component) and variation in living conditions between different habitat types (spatial component). Similar between these two forms of variation is that they constitute variability in external factors, the environment, that influence the performance of individuals.

Environmental variation can be either deterministic or random. All natural populations exhibit both a deterministic and a random part in their population dynamics (Lande et al., 2003), but their relative magnitude can differ. Examples of deterministic variation are cyclical environmental states, for example from seasonal variations or long term climate cycles, or deterministic trends. The characteristic of random variation, or random processes, is that the next state of the system is not fully determined by the previous steps. In more technical terms a stochastic process can be described as a statistical phenomenon that evolves in time according to probabilistic laws (Chatfield, 2004). Relating to population dynamics, this means that random variation in the environment introduces uncertainty into the fate of individual populations, and this uncertainty is what is meant by environmental stochasticity. In the ecological literature, environmental stochasticity is usually reserved for the uncertainty introduced by temporal variation, while the uncertainty stemming from spatial variation in the environment is labelled environmental heterogeneity or spatial heterogeneity (Begon et al., 1996). However, some authors use the term "environmental variation" to represent a combination of temporal and spatial variation (White, 2000).

Environmental stochasticity can be realized as fluctuations around a mean or coupled to deterministic cycles or trends. Stochastic processes can also have a non-stationary mean and therefore exhibit apparent trends or cyclic behaviour. If true stochasticity exists is an open philosophical question. The stochastic component in a process can either be seen as lack of information, where the stochastic noise component represents an error term to our knowledge, or as an inherent part of the process. If we believe that stochasticity is an inherent part of the process, we are also subscribing to a stochastic view of the world, as opposed to a deterministic one. As a side note it can also be mentioned that deterministic chaotic systems can, from a practical point of view, be indistinguishable from genuine stochasticity (Chatfield, 2004). It is also important to keep in mind that environmental stochasticity can be considered on multiple scales (Pimm, 1991), even if the default in population models, for practical reasons, often is seasonal or yearly fluctuations.

Before we can go into the question on how environmental stochasticity is related to extinction risk, another clarification is in place. The variation that cause environmental stochasticity by definition stems from factors external to the species itself, and can include climatic factors

such as rainfall or temperature, but also biotic factors such as predators (Begon et al., 1996) . However, the variation most often measured and used to represent environmental variation is in population growth rate or in species traits, such as birth rates or survival (Morris & Doak, 2002). This means that the measured variation is actually the environmental variation filtered through the biology of the species, with its typical physical tolerances and behavioural responses (Hubbell, 1973; Roughgarden, 1975; Laakso et al., 2001). This is often reasonable and even preferable, since it means that many types of environmental fluctuations, some of which we might not even be aware of, are integrated and translated into the parameters relevant for the population growth of the species at hand. However, it has been shown (Laakso et al., 2001) that this filtering can transform the noise signal, so it cannot be taken for granted that the type of variation observed in the environment, with regards to temporal correlation structure and amplitude, is the same that can be found in the vital rates.

Demographic stochasticity

Variation in vital rates or population sizes due to fluctuations in the environment is easy to grasp. We can all see how seasons come and go, and how environments change over time. From that point the step is quite short to understand that these fluctuations will influence the organisms that inhabit this environment, and that the fluctuation will, at least partly, transcend into the population dynamics of these organisms. Demographic stochasticity might not be as intuitive.

Demographic stochasticity is usually defined as the variation in population growth rate, or other measures of population performance, caused by random variation in individual fates within a year (May, 1973; Soulé & Wilcox, 1980; Lande 1993; Morris & Doak 2002; Kendall & Fox, 2002). The classic example is to compare an individual fate to a coin toss, and that the demographic stochasticity corresponds to the variation in the number of heads and tails obtained from a fixed number of coin flips. Analogous to coin flips, an individual either survives or dies with a certain probability, but for a small sample the outcome may deviate substantially from the expectation. Therefore the strength of demographic stochasticity is inherently dependent on population size, becoming stronger with decreasing population size. A simple example can be constructed by envisioning a population of 5 individuals, each with a chance of surviving of p=0.6 The expected number of survivors the next year is 3 (0.6*5). However, there is still a possibility that the population goes extinct due to chance with a probability of about 1% $(0,4^5)$, and a probability of about 32% that the population will be smaller than the expected number of 3. With a population of 2 individuals the probability of extinction is 16%. Several years of bad luck can also follow in a row, and cause population extinction. Variation in reproduction naturally also results in variation in population growth rate, but in contrast to survival the individual outcome does not necessarily have to be an all or nothing affair. Taking the example of a bird nest, the expected clutch size might be six eggs, but with a range between two and eight eggs, with each possible outcome having a certain probability. Thus, in the same way as survival, pure chance can cause the annual reproduction in a population to deviate from the expectation, and this is more likely in small populations.

When demographic stochasticity is compared to coin flips (Morris & Doak, 2002) another aspect is ignored, namely explicit individual variation in demographic rates. This is sometimes labelled individual heterogeneity (Conner & White, 1999). If demographic stochasticity in the first case corresponds to variation due to coin flips with fixed probabilities of outcomes, this second case would correspond to coin flips with varying probabilities. These two aspects of demographic stochasticity correspond to the difference between variation due

to sampling and variation due to structured differences between individuals. More generally, structural differences appear when an individual's demographic traits is not independent and identically distributed (idd). This is the situation both when there are correlations among individuals at a certain time or within individuals over time (Kendall & Fox, 2003). One example of correlations among individuals is compensation in survival rate due to how other individuals in the population are doing. Correlations within individuals over time occur when some individuals are fundamentally "better" than others over the course of their lives (Conner & White, 1999). Naturally, structured differences can occur in fecundity or other traits as well.

Other aspects of the life cycle where demographic stochasticity can manifest are variation in sex ratio and in the mating system. Examples include pair formation and territoriality. Gabriel & Ferrière (2004) label these sorts of interactions *Interaction stochasticities* to distinguish them from the stochastic effects arising only from variation in individual fate. Engen et al. (2003) proposed a method to calculate the effect of mating system on the magnitude of demographic stochasticity.

Stochastic population models

My aim here is not to give a full account of all possible models that can be used to study stochastic population growth. The cliché states that there are as many models as there are modellers, which would make it hard, to say the least, to give a full account of how to model stochasticity. I will rather present some common approaches to population modelling, and show how they differ from each other. Important to remember is that many applications of stochastic models use simulations, where each model run only represents one possible outcome, and therefore many replications are needed to form probabilistic statements of e.g. population viability or which traits are most important for the population growth rate (Beissinger & Westphal, 1998). Which modelling approach will fit a particular study depends on the aim, the research questions posed, and on knowledge of the system. For fuller accounts of stochastic population models see, for example, Tuljapurkar & Caswell (1997), Caswell (2001), Morris & Doak (2002) and Lande et al. (2003).

(1) Diffusion approximations

The use of diffusion approximations (DA) (Cox & Miller, 1965) to model population dynamics were introduced in the 70's (May, 1973; Ludwig, 1976 ; Leigh, 1981; Tuljapurkar, 1982; Lande & Orzack, 1988). The basic premise is that a stochastic population in discrete time can be adequately described by a diffusion process that is continuous in population size and time (Lande et al., 2003). This represents a Brownian motion with drift. The diffusion approximation is a powerful way to derive analytical approximations of the distribution of quasi-extinction times and the cumulative distribution of extinction times, and models can include both environmental and demographical stochasticity. It has mainly been used for unstructured models built on count data (Ludwig, 1976; Leight, 1981), but Lande & Orzack (1988) showed that the diffusion approximation works fairly well for describing structured models, even if the age or stage-structure produces autocorrelation in N(t), which violates assumptions of independence. An assumption in diffusion models is that the environmental influences are small to moderate, and that the population size changes in small increments, so these conditions must be checked. The two parameters needed to derive the DA for the population, μ and σ^2_μ, can be estimated by linear regression from a population time series at $t_0, t_1, t_2 \dots t_k$, as shown by Dennis et al (1991).

Using the DA the probability density function for reaching the quasi-extinction threshold at time=t can be obtained by (From Lande & Orzack (1988) and Morris & Doak (2002)):

$$G\left(t \mid \mu, \sigma_\mu^2, X_0, c\right) = \frac{X_0 - c}{\sqrt{2\pi\sigma_\mu^2 t^3}} \exp\left(\frac{\left(-X_0 - c + |\mu|t\right)^2}{2\sigma_\mu^2 t}\right)$$

Where X_0 is the starting population size, c is the quasi-extinction threshold, μ is the population growth rate, and σ_μ^2 is the variance in μ. A visualization of this function is shown in Fig 1,a. The probability density function can be integrated to obtain the cumulative distribution function for the time to quasi-extinction (Fig 1,b).
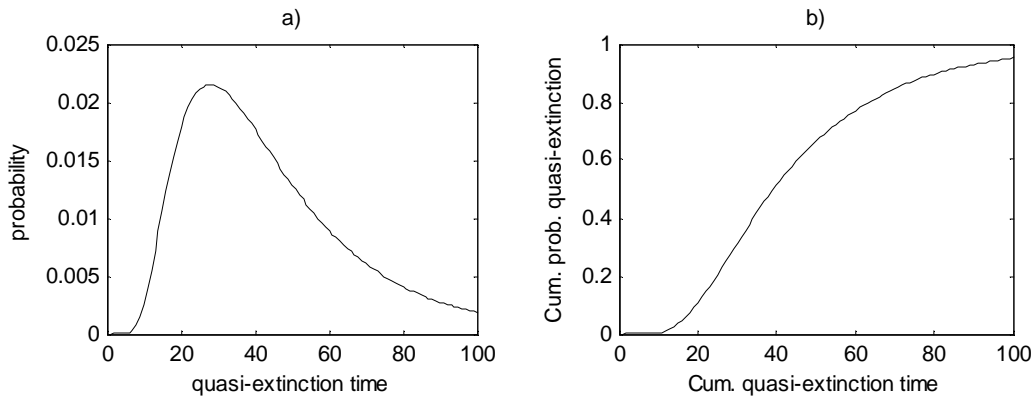

Fig. 1. Quasi-extinction times using the DA. a) Probability of hitting the quasi-extinction threshold at time=t. b) Cumulative probability of quasi-extinction. μ=-0.05, σ^2=0.04, N0=100, Nx=10.

Even though DA models make many simplifying assumptions Sabo et al. (2004) showed that they still can produce fairly accurate estimates of extinction risk. It their study, Sabo et al. simulated population trajectories from stochastic models with different assumptions on the form of density dependence, and then estimated DA parameters from the first half of these trajectories. The extinction risk from the DA model was then compared to the observed extinction risk. The DA was most successful in predicting extinction risk for simple forms of density dependence (ceiling model) and high risk of extinction (75%), and less so with more complex forms of density dependence (Beverton-Holt & Ricker). The DA also produces biased estimates of extinction risks, generally underestimating risk at lower levels of actual extinction risk (50%) and overestimating risk at higher levels actual of extinction risk (75%). The largest errors occurred when populations showed strong recoveries and started far from carrying capacity, which yielded overtly optimistic estimates of extinction with the DA. However, Sabo et al. conclude that DAs is still a useful tool, especially when there is a lack of detailed population data, preferable used to make relative comparisons between populations or species. Many of these issues with the DA have also been pointed out by other authors (e.g. Lande et al., 2003; Holmes, 2004).

(2) Unstructured population models (Count or census based models)

Models tracking population counts have been used extensively to study population dynamics (May, 1973; Dennis, 1991; Morris & Doak, 2004), and can include stochastic factors. They are often the choice when there only are count data of population sizes, and no explicit

demographical information, or when there is no reason to believe that groups of individuals differ in their vital rates. One large advantage with unstructured models, compared to e.g. structured matrix models (see below), is that they use relatively few parameters, i.e. are simpler, and therefore require less data to be parameterized. For endangered species for which we lack information, they are often the only option. Unstructured models can easily be made to include environmental variation, and there exist several ways to include density dependence as well. Engen et al (1998; also Lande et al., 2003) has developed methods for including both environmental and demographic stochasticity in unstructured population models, by partitioning the variance in population growth rate by their relative contributions. However this approach requires a demographic mark-recapture study, beside the count data.

Unstructured models can be based on discrete difference equations, such as the discrete version of the logistic equation or the Ricker equation, or on continuous differential equations.

(3) Structured population models

In populations where the individuals differ in their contribution to population growth a structured model is suitable. The structure implied can be in age, life stage, size or other population structures. The classical way to deal with this is through matrix models (Leslie, 1945; Caswell, 2001). The basic form of a stochastic matrix model is:

$$\overline{n}(t+1) = A(t) * \overline{n}(t)$$

Where A(t) is the transition matrix at time t and $\overline{n}$ represents the population vector at time t. If the transition matrix is the same at all time steps and demographic stochasticity is omitted, the model is fully deterministic. Otherwise, if the transition matrices vary, this can represent periodic fluctuations in the environment, environmental stochasticity or other factors. For deterministic or periodic models there exist analytical methods, but for stochastic matrix models the solution is usually simulation. They can however be accompanied by analytical tools such as the diffusion approximation (Lande & Orzack, 1988; Caswell, 2001). Matrix models can incorporate almost any population process, and can therefore be built to depict highly complex population models. Beside environmental and demographic stochasticity, factors such as density dependence, correlation between vital rates and spatial heterogeneity can all be included in a matrix model. However, in most cases the limiting factor for building complex models is the availability and quality of data (Burnham & Anderson, 1998; Morris & Doak, 2002)

Either way, matrix models are suitable for building stochastic simulation models that include both demographic and/or environmental stochasticity. Environmental stochasticity can be included by using a Markov chain model of environmental states (expressed as fixed matrices), by drawing independent and identically distributed sequences of environmental states, as AR(I)MA models, or as a Monte Carlo simulation of vital rates at different time steps. Demographic stochasticity can be considered in a multitude of ways, from the relatively simple case of drawing survival outcomes from a binomial distribution to complex individual based models (i-state configuration models).

There also exist other analytical tools to deal with population structure. Partial differential equations describe individuals as a continuous function of e.g. age or size (Caswell, 2001). Delay-differential equations are more similar to matrix models, since they also divide the individuals into discrete states, and use several coupled differential equations with time lags

to model the population dynamics (Caswell, 2001; Murray, 2002). Both these modelling approaches are based on differential equations and therefore function in continuous time, compared to the discrete time approach of matrix models, and are therefore more suitable for populations with continuous growth and overlapping generations. Stochastic differential equations (SDE) are the random counterpart of differential equations, and can be also be used to model structured populations (Caswell, 2001).

(4) Branching processes

Branching processes is an analytical method that can be used for studying demographic stochasticity. The methods were discovered by Francis Galton and Henry Watson in 1874, when they examined the extinction of family names. Branching processes are basically a way to study the proliferation and extinction of lineages, where individuals produce new individuals according to a probabilistic rule (Caswell, 2001). In the case of Galton & Watson they were interested in the extinction of lineages carrying a family name (descendents from one ancestor), while we are more interested in the extinction of all lineages at the same time, i.e. population extinction. The analytical results that can be obtained from branching processes include expected population size, stochastic sensitivity of extinction probability from changes in vital rates, and lineage extinction probability over time. Two examples of use of branching processes can be found in Kokko & Ebenhard (1996) and Fujiwara (2007).

Modelling environmental variation

If a population model is to include environmental variation there are several decisions to make, no matter the model specification, or if the model is structured or unstructured. First of all it must be decided how and where environmental variation enters in the model. If the variation is measured in the population growth rate or in vital rates, it is natural to model the environmental stochasticity in these traits as well. This can be accomplished by randomly picking population growth rates (Lande, 1993), matrices (Menges & Dolan, 1998; Fieberg & Ellner, 2001), matrix entries and vital rates (Doak et al, 1994; Oro et al., 2004; Krüger, 2007), or other traits that describe the environmental variation expressed by the population to be modelled. However, other possible ways to include environmental stochasticity exist, for instance to express it through variation in the carrying capacity (e.g. Roughgarden, 1975; Morales, 1999) or by directly manipulating expected population size (Iwasa, 1988). Another option is to model the environmental variation directly and link this to population traits through functional relationships (Meyer et al., 2006; Vasseur, 2007). Environmental stochasticity can also be expressed through catastrophic events and bonanzas at certain frequencies (Lande, 1993; Mangel & Tier, 1993), while either including or excluding "normal" variation. It has however been argued that catastrophic events should be seen as part of a continuum of environmental variation, and not as a separate process (Lande et al., 2003). How and if catastrophes are to be included depends in part on the time span considered, but also on the question you are trying to answer. In general, the imperative to model catastrophes increase with longer time spans, since it is likely that they will be an important part of the dynamics.

It must also be decided if the environmental variation is modelled as correlated or uncorrelated. Uncorrelated variation implies that the environmental states are independent and identically distributed (iid), and this type of variation corresponds to a white noise process. If the environmental variation is correlated, either in the form of periodic cycles or in the form

of random correlations (or a mix of the two), more considerations are needed. If the system exhibit periodic cycles it must be decided if these are to be modelled purely deterministically, or if there is a random factor as well. For random correlated variation it must be established what form of correlation structure is appropriate. Correlation structure of time series can both be analysed with regression techniques and by spectral analysis of the correlogram and the spectral density function (Chatfield, 2004; Lande et al., 2003). There exist a number of ways to model correlated temporal variation, each with different assumptions. The simplest way is probably to use an autoregressive function (Ripa & Lundberg), but recently $1/f^\beta$ noise has been claimed to better capture the characteristics of natural environmental variation (Halley, 1996). In $1/f^\beta$ noise the contribution (power) of different frequencies to the total variance is scaled through the $1/f^\beta$ relationship, where f represents the frequency and β is the spectral exponent. Time series mainly determined by low frequency fluctuations is represented by $\beta > 0$, and with $\beta = 0$ the fluctuations are frequency independent (Halley, 1996). It should be noted that in opposition to autoregressive variation (and uncorrelated white noise), $1/f^\beta$ is non-stationary, so the variance of the time series increase with time and the time series does not have a mean value around where it fluctuates (Halley, 1996; Halley & Inchausti, 2004).

There exist many statistical tools to estimate environmental variation from empirical data. For census data, variation in population size can be estimated by linear regression methods (Dennis, 1991). These methods can be extended by non-linear regression to separate influences from density dependence and environmental variation (Morris & Doak, 2002). It is generally claimed that not taking density dependence into account when present, will overestimate the environmental variation and underestimate the population growth rate (Ginzburg et al., 1990; Morris & Doak, 2002), however the relationships might be more complicated (Henle et al., 2004). In structured models, the environmental variation should be estimated for all matrix elements or vital rates, if the data set is large enough to do so. Depending on the type of data and census there are a number of methods to choose from to measure survival and its variance, ranging from logistic regression or log-linear models (Morris & Doak, 2002) to maximum likelihood methods for mark-recapture data (Lebreton et al., 1992; White et al., 2002). In matrix models, an estimate of environmental variation can also be introduced by letting each year's matrix represent an environmental state, and by randomly picking matrices (Caswell, 2001; Fieberg & Ellner, 2001). An advantage with this method is that the within year correlation structure between vital rates is preserved, however very rigidly (Morris & Doak, 2002). A disadvantage is that if the number of yearly transition matrices is few it is likely that the variation in vital rates is underestimated, and hence persistence overestimated (Akçakaya, 2000).

To allow the vital rates to vary continuously in a structured simulation model, a parametric approach should be used (Fieberg & Ellner, 2001). However, this introduces another problem. To generate single random vital rates from the appropriate distributions is fairly straightforward, but then the covariation structure is lost. To impose a within year covariance can other the other hand change the probability distributions of the vital rates (Caswell, 2001; Morris & Doak, 2002). Morris & Doak (2002) present a method that uses the mapping of multivariate normal distributions onto beta distributions, to construct correlated vital rates.

Since raw estimates of environmental variation are influenced by sampling variation, this component should be subtracted to obtain an unbiased estimate of environmental variation. Engen et al (1998) presents a method to partition the environmental and demographic variance, and since demographic variance is a type of sampling variation this method works in both cases. White (2000) extended this method to remove sampling variation, by allowing the sampling variance to differ between years. A further discussion of this can be found in Morris & Doak (2002). For binomially distributed vital rates such as survival Kendall (1998)

developed a method to remove sampling variation, by combining a beta distribution for the survival rate with the binomial distribution for the chance of seeing a certain number of survivors. However, while estimates of environmental variation can be inflated by not separating sampling variance, a larger problem is usually that most population studies are too short to properly estimate the environmental variance. Arinõ & Pimm (1995) examined a large number of long-term population counts and found that for most of them the variance in annual numbers increased with the length of the period used to estimate variance. This has two main consequences; the first being that for short term studies we underestimate the variability in demographic traits and population variability. Secondly, long term studies are needed if we want to pick up cyclic behaviour and temporal correlations of long period. Also, rare events, both in the form of catastrophes and bonanzas, are often not included in the observation series or with poorly estimated frequencies, which leads to underestimation of the environmental variation (Pimm, 1991; Ludwig, 1999; Coulson et al., 2001).

Modelling demographic stochasticity

As I mentioned earlier, demographic stochasticity is usually modelled simply as a sampling effect, and by using the appropriate statistical distribution. For survival this usually equates to the binomial distribution (Caswell, 2001), for reproduction there are a number of distributions to choose from. The application is straightforward, and most PVA models use this formulation of demographic stochasticity (Beissinger and McCullough 2002; Morris & Doak, 2004). Demographic stochasticity can also be modelled directly on population size by making it a Poisson variable, with the expected population size as mean (Iwasa, 1988).

If demographic stochasticity is modelled as a sampling effect for fixed vital rates, the second aspect of demographic stochasticity, i.e. individual variation in vital rates, is ignored. This is usually the case for stage or age structured matrix models (e.g. Gaona et al, 1998; Heino & Sabadell, 2003), where individuals within groups are considered homogenous (Caswell, 2001). However some individual variation is accounted for by dividing individuals into several classes, which is one of the main advantages with structured models compared to unstructured ones. Individual heterogeneity can be explicitly modelled by using an individual based model (i-state configuration model) (Grimm et al, 2006) where the vital rates for each individual are drawn from probability distributions that describe the variation within the class (Letcher et al, 1998; Schiegg et al, 2006).

In the case of individual survival the outcome follows a binomial distribution, since survival has a binary outcome. With traits such as reproduction, where there is an expected mean number of offspring with individual variation around this mean, a Poisson lognormal or negative binomial distribution is usually more appropriate. Which distribution to use for reproduction depends on the system though, and there are several candidates to consider (Morris & Doak, 2002). A careful examination of empirical data may here act as a guide to which distribution to assume. It should also be noted that the reproduction function can be composed of several parts, each connected to a certain type of randomness (Caswell, 2001). For birds, the number of offspring produced can be the product of the underlying vital rates; breeding probability, clutch size, fledgling success and first year survival. Then it might be suitable to explicitly model the number of breeders and first year survival as binomial processes, and the number of chicks as a Poisson process, however this can greatly slow down a simulation program.

Stochastic extinction dynamics

Environmental variation and extinction risk

Environmental stochasticity increase the extinction risk compared to a constant environment. The most immediate effect of environmental variation is that populations can go extinct by chance, even if the stochastic population growth rate is positive, as seen in fig?. Secondly, since population growth is a multiplicative process, the stochastic mean population growth rate is estimated by the geometric mean and not the arithmetic mean. From this follows that the stochastic mean population growth rate (λ_s) is less that the deterministic population growth rate for the mean environment. In short: environmental variation decrease population growth rate, compared to a constant environment. For structured populations, the same result can be seen from Tuljapurkar's approximation (Tuljapurkar, 1982) of the stochastic growth rate (λ_s). If the environmental states are independent then:

$$\log \lambda_s \approx \log \lambda_1 - \frac{\tau^2}{2\lambda_1}$$

where

$$\tau^2 = \sum_{i=1}^{s} \sum_{j=1}^{s} \sum_{k=1}^{s} \sum_{l=1}^{s} Cov(a_{ij}, a_{kl}) \overline{S}_{ij} \overline{S}_{kl}$$

Here λ_1 is the deterministic population growth rate for the mean environment, $Cov(a_{ij}, a_{kl})$ is the covariance between matrix entries a_{ij} and a_{kl} and S_{ij} is the sensitivity of matrix entry i,j. Since τ^2 cannot be negative this formula shows us that environmental variation decrease the stochastic growth rate, compared to the average environment.

Using diffusion models Lande (1993) showed that for positive growth rates, the average time to extinction scales to carrying capacity as a power law by $T(K) \approx 2K^c / (V_e c^2)$, where $c = 2\overline{r}/V_e - 1$, the mean population growth rate is $\overline{r}$, and environmental variance is V_e. For negative growth rates the approximation is:

$$T(K) \approx \frac{-\ln K - 1/c}{\overline{r}}$$

This means that the mean time to extinction scales will scale faster than linearly to K if $\overline{r}/V_e$ is above 1, and slower if it is below 1.

As mentioned above, catastrophes are often viewed as separate from "normal" environmental variation, or environmental variation is modelled only as catastrophes (Lande, 1993; Mangel & Tier, 1993). It has been pointed out that the inclusion of catastrophes have a tremendous effect on the persistence time of species' (Mangel & Tier, 1993), but that is often in comparison to models that only consider demographic stochasticity. Then it is not very surprising that the extinction risk increase dramatically. Lande (1993) shows that the average extinction time scales as a power law with carrying capacity, both for models with environmental stochasticity or catastrophes, and that their relative importance depend on the magnitude of environmental variance and the strength and frequency of catastrophes. Maybe a more interesting comparison is between extinction risk in models with environmental variation obtained from short time series, and expressing "normal" variation, and models with

environmental variation from long time series, expressing the full scope of variation and rare catastrophic events. The general observation that population persistence is strongly influenced by rare events is however an important one.

In structured models the impact of environmental variation on population extinction risk as mediated through particular vital rates, is conditioned on the life history. This means that general quantitative statements of how important e.g. variation in fecundity is to determine extinction risk cannot be made. For instance, high adult survival between years lessens the impact of environmental variation in fecundity on population growth rate (Saether et al, 2002), and resembles an iteroparous, "slow" life history. This stems from the fact that adult survival buffer population size during years of low fecundity, and the pattern can also be understood by noting that the population growth rate has a low sensitivity to changes in fecundity. On the other hand a semelparous "fast" life history is most sensitive to variation in juvenile survival and developmental rate (Jonsson & Ebenman, 2001). Similar arguments can be made for other vital rates, and species are in fact expected, at least to some extent, to evolve life history syndromes to lessen the impact of temporal variation in certain vital rates.

So far I have only considered how environmental variation per se will influence population growth rate, and hence extinction risk. What about different types of environmental variation? Environmental variation can be distributed in several ways (Fig. 2), ranging from temporally uncorrelated white noise to highly correlated black noise. The variation can also exhibit negative autocorrelation, which correspond to blue noise. The first studies on extinction risk that included environmental variation assumed white noise (Lewontin & Cohen, 1969; Feldman & Roughgarden, 1975; Leigh, 1981; Tier & Hanson, 1981; Lande & Orzack, 1988; but see Tuljapurkar, 1980), probably since it is a reasonable null hypothesis and it does not require many other assumptions. When temporal correlation was started to be acknowledged, it was usually deemed detrimental to populations. Lawton (1988) presented this argument: since consecutively bad years are more likely with correlated noise, this will increase the risk of extinction, since a population is less likely to survive a series of years with bad conditions, compared to single bad years. Therefore, noise that show positive temporal correlation should result in a higher extinction risk compared to white noise (Lawton, 1988; Halley, 1996). More recent concerns have been raised that the assumption of uncorrelated environmental variation might seriously influence the estimates of extinction risk (Johst & Wissel, 1997; Halley & Kunin, 1999), especially in relation to PVA:s. If the assumption of white noise indeed cause bias in the estimates of extinction risk, then an obvious question arise; what sort of bias? Does white noise result in overtly pessimistic or optimistic estimates of extinction risk?

Some theoretical studies that have compared random white noise to correlated noise has supported the view that temporally correlated noise increase the risk of extinction (Johst & Wissel, 1997; Inchausti & Halley, 2003), but other show contradictory results (Ripa & Lundberg, 1996). It is apparent that the modelling approach (Morales, 1999), the strength and type of density dependence (Petchey et al, 1997; Morales, 1999, Heino et al, 2000), the time scale (Halley & Kunin, 1999) and the scaling of variance (Heino et al, 2000; Wichmann et al, 2005) all interact with noise colour when influencing the extinction risk, but to complicate things further, so does life history (Heino & Sabadell, 2003). Many researchers have shown that in a population model with overcompensatory population dynamics, a reddened noise spectrum will decrease the extinction risk compared to white noise, while it will increase with undercompensatory dynamics (Petchey et al, 1997; Cuddington & Yodzis, 1999; Heino et al, 2000). Johst & Wissel (1997) assumed constant population growth rate up to a population ceiling, which implies undercompenstory dynamics, so their result is in line with this observation as well. Red noise also increases the variability in population fates, which suggests that the fate of particular populations will be harder to predict (Cuddington &

Yodzis, 1999). Heino & Sabadell (2003) examined how the life history interacts with noise colour, using a structured population model. They modelled four simplified life histories ranging from annual, semelparous biennial, iteroparous biennial, and perennial, and came to the conclusion that the extinction risk of annuals decrease with temporally correlated noise. The opposite pattern was found for iteroparous biennials and perennials, with the semelparous life history somewhere in between. This means that "slower" life histories, such as iteroparous modes, are negatively affected by a reddened environmental variation. However, the approach of Heino & Sabadell is very simplified, and does not differentiate between iteroparous species in the fast-slow continuum. From a conservation biology viewpoint it would be interesting to know how different life-history types, categorized e.g. by survival, fecundity, age at first reproduction and population growth rate are affected by different noise colours.
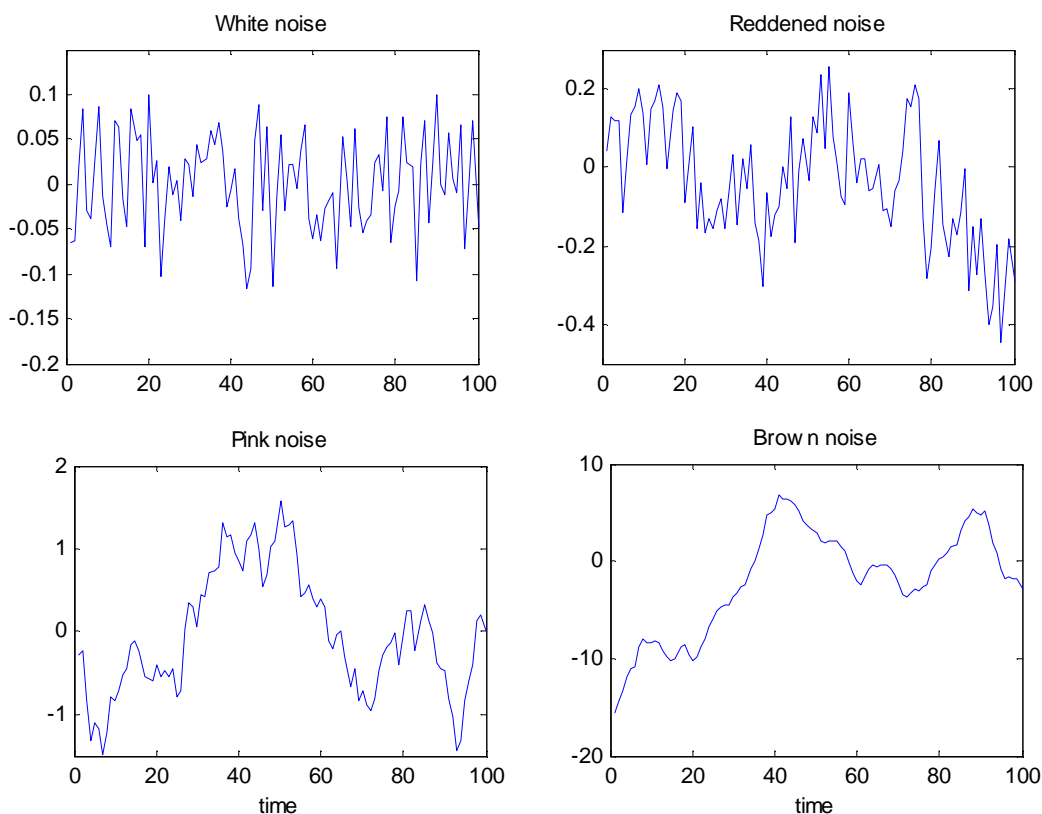

Fig. 2. Time series with increasing amounts of temporal autocorrelation, constructed with $1/f^{\beta}$-noise. From top left to bottom right the β values are 0, -0.5, -1, -2.

Recently it has been noted that the frequency distribution of the environmental noise is an important factor in determining extinction risk (Schwager et al, 2006). They point out that the risk of catastrophic events and the risk of a run of bad years must be considered separately to understand the effect of noise colour. If catastrophes are viewed as part of the continuum of environmental variation, then on a fixed time scale the risk of catastrophes decrease with increasing noise colour, while the risk of a run of bad years increase (in line with Lawton's argument). This is due to the fact that while the probability of "catastrophic conditions" at time t+1 is the same at all time steps under white noise, it is depending on the conditions at time t under correlated noise. A catastrophe can basically strike at once under white noise conditions, while it tends to approach by drift under temporally correlated conditions. This also explains why the risk of a run of bad years increases with increasing noise colour. Many

of the previous studies have made different assumptions on these two factors, and this probably explains some of the contradictory results.

The next obvious question is whether reddened or white noise is most common in nature? Naturally this differs depending on what environment or trait that is under study. The reason why the relation between noise colour and extinction risk has been studied so much lately, is the strong evidence that time series of environmental variation are generally temporally correlated (Pimm & Redfern, 1988; Ariño & Pimm, 1995; Inchausti & Halley, 2002). In a comparison between several time series of environmental variables Vasseur & Yodzis (2004) show that the temporal correlation seems to differ between environments, with marine environments having red-brown spectra and terrestrial environments showing pink spectra. They also find a difference between coastal and inland terrestrial environments, with coastal areas having redder spectra. That there are differences are not unexpected, but the observation is important since it forces researchers to consider what type variation can be found in their system. However coloured environmental noise does not necessarily lead to coloured population dynamics. Conversely many mechanisms beside coloured environmental noise can lead to coloured population dynamics, e.g. time delays, stochastic density dependence, and spatial interactions (Lundberg et al, 2000; Greenman & Benton, 2005; Vasseur, 2007). In an experimental study on ciliates Petchey (2000) showed that the dynamics of all populations showed reddened dynamics, regardless of environmental colour. This indicates that the colour of population dynamics depend on intrinsic factors. More research is needed in this area to separate the effects of environmental forcing and internal factors.

Demographic stochasticity and extinction risk

The basic effect of demographic stochasticity is to introduce the risk of population decline or population extinction, even in a population with positive growth rate. Populations naturally consist of discrete entities, and demographic stochasticity is the consequence of small population size and discreteness (Halley & Iwasa, 1998). Since it is a problem of small populations, demographic stochasticity has been studied extensively in relation to species conservation (e.g. May, 1973; Richer-Dyn & Goel, 1972; Lande, 1993). However, the effect of demographic stochasticity decrease fast with population size, and Richter-Dyn & Goel (1972) noted that in a population with a ceiling of 40 individuals and positive population growth, the mean extinction time is in the order of tens of thousands to millions of generations. When the population growth is positive, mean time to extinction in a model with demographic stochasticity scales exponentially with carrying capacity (Richter-Dyn & Goel, 1972; Leigh, 1981; Lande, 1993). Early studies concluded that demographic stochasticity can be ignored for population sizes larger than 100 (Lande, 1993), which has subsequently often been used as a quasi-extinction threshold (Morris & Doak, 2002). The reasoning is then that demographic stochasticity can be ignored in the model, if the quasi-extinction threshold is set high enough. It has however been pointed out that the cut-off is somewhat arbitrary (Morris & Doak, 2002), and that depending on the life-history and breeding system of the species demographic stochasticity can play a role at larger population sizes (Kokko & Ebenhard, 1996; Gilpin, 1992). Kokko & Ebenhard (1996) launched the concept of demographic effective population size (N_D) to determine the range of population sizes where demographic stochasticity cannot be ignored. Fluctuations in the sex ratio will also increase the demographic stochasticity, and this effect is enhanced in long-lived species where there is a temporal correlation in the sex ratio (Engen et al., 2003). It should be noted that both these studies include interaction stochasticities, as well as ordinary demographic stochasticity.

The next step is to consider the stochastic effects on extinction risk from differences between individuals. As mentioned above, there are two types of individual differences to consider; unstructured and structured differences. Remember that the distinction corresponds to assuming that individuals are either the same with respect to survival rate and fecundity, or with fundamental differences. Kendall & Fox (2002) show that for survival, which is a binomial process, unstructured differences in survival does not affect demographic variance (the variance in population growth rate that is caused by demographic stochasticity), and hence extinction risk, compared to assuming that all individuals are the same. This does not hold for fecundity, where unstructured individual variation can affect demographic variance (Robert et al., 2003; Kendall & Fox, 2003). The exact relationship depends on which trait distribution that is assumed, but in Poisson-distributed fecundity unstructured variation will increase the demographic variance and therefore the extinction risk (Kendall & Fox, 2003).

Turning to structured differences, the situation is a bit different. For survival, assuming binomial variance, it has been shown analytically that structural differences leads to lower levels of demographic variance (White, 2000; Kendall & Fox, 2003). However this is not true for fecundity, when a Poisson distribution is used to assign individual trait values. In that case the demographic variance, and hence extinction risk, is not affected by structured individual variation (Kendall & Fox, 2002).

To conclude and summarise the discussion on demographic stochasticity and individual differences, it can be said that the affect on extinction risk from individual variation in demographic traits depends on the model specifications. For survival, unstructured variation does not affect extinction risk, while structured variation decrease it. For fecundity, unstructured variation increase extinction risk, and at the same time structured variation does not affect extinction risk. This does only hold for Poisson distributed fecundity though, so for models that utilise other distributions the relationship can be different.

Variation in sensitive traits

As mentioned earlier, a common generalisation in stochastic demography is that temporal variation in vital rates will decrease the population growth rate compared to a static environment (Pfister, 1998; Doak et al, 2005), and thereby increase the extinction risk. Therefore it has been postulated that species should not vary much in the vital rates that are sensitive to population growth, so matrix elements with the largest sensitivity values should also be under the strongest selection for low variance (Pfister, 1998; Caswell, 2001; Jonsson & Ebenman, 2001). This generalisation is also based on Tuljapurkar's approximation (1982; 1990) for the stochastic log growth rate, from which follow that:

$$\frac{\partial(\log \lambda_s)}{\partial \operatorname{var}(e_{k,l})} \approx \frac{-1}{2\overline{\lambda}_1^2} \overline{S}_{e_{k,l}}^2$$

$$\frac{\partial(\log \lambda_s)}{\partial \operatorname{cov}(e_{k,l}, e_{m,n})} \approx \frac{-1}{2\overline{\lambda}_1^2} (\overline{S}_{e_{k,l}} \overline{S}_{e_{m,n}})$$

where $e_{i,j}$ is matrix element (i,j), $\overline{S}_{e_{k,l}}$ is the sensitivity of matrix element $e_{i,j}$ for the mean matrix, and $\delta(\log\lambda_s)/\delta\operatorname{var}(e_{i,j})$ is the sensitivity of $\log\lambda_s$ to changes in the variance of $e_{i,j}$. Since the sensitivities of matrix elements are always positive, the sensitivity of $\log \lambda_s$ to variances

or covariances are always negative. This means that the population growth rate, lambda, will always decrease with increasing variances and covariances in the matrix elements. Sensitivities are generally perceived as selection gradients (Lande, 1982; Johnson & Ebenman, 2001), so traits for which the sensitivity of log λ_s to the trait variance is large and negative, should be under strong selection for decreased variance. This prediction has been tested by Pfister (1998), and she found a negative correlation between the sensitivities and the variances of matrix elements. This means that species seem to be demographically buffered against environmental variation. On the other hand, a consequence of such a relationship is that species, in response to changes in their living conditions, will have problems to evolve in the vital rates that influence their population growth rate the most. This can lead to difficulties for species to adapt their life-history to changes in their habitat, for example due to anthropogenic influence.

It has later been pointed out that Tuljapurkar's approximation assumes that the variance and covariance terms of matrix elements are independent (Doak et al., 2005). This is clearly incorrect for many natural systems. Doak et al. recast Tuljapurkar's approximation in terms of the actual vital rates and show that the sensitivity of log λ_s to the variance in a vital rate v_i is dependent on both the deterministic sensitivities of the vital rates and the correlation between v_i and other vital rates.

$$\frac{\partial(\log \hat{\lambda}_s)}{\partial \sigma_i^2} \approx \frac{-1}{\overline{\lambda}_1^2}\left(\overline{S}_{v_i}^2 + \sum_{j \neq i} \overline{S}_{v_i}\overline{S}_{v_j}\sigma_{v_j}corr(v_i,v_j) \right)$$

Where σ_{vj} represent the standard deviation in trait v_i and corr(v_i, v_j) is the correlation between traits v_i and v_j. The expression found after the summation shows us that if v_i has sufficiently strong negative correlations to other vital rates with high variances and sensitivities, then the sensitivity of log λ_s to variance in v_i can be positive. This means that selection will favour high variation in that vital rate, and that the population growth rate is higher with high variation in v_i. The condition that governs if the sensitivity will be positive is:

$$-\sum_{j \neq i} \overline{S}_{v_j}\sigma_{v_j}corr(v_i,v_j) > \overline{S}_{v_i}\sigma_{v_i}$$

As a result the population growth rate can increase with increased variation in vital rates under the right circumstances. Doak et al (2005) apply this corrected formula to Desert tortoise data, and show that selection for high variability in vital rates can indeed occur.

Experimental support for theoretical predictions

There is no doubt that environmental and demographic stochasticity influence populations, and the question is rather how large their relative importance and influence are, compared to other factors. Since the experimental investigation of the effects of stochasticity needs many replicate populations, they are very hard to study. The need for multiple replicates also means that these studies cannot be performed on rare or threatened populations. However, a number of experimental studies have tried to partition the effects of stochastic factors on population extinction risk.

Drake (2006) and Drake & Lodge (2004) studied Daphnia populations in mesocosms and found a pronounced peak in the distribution of extinction times early in the experiment, but no

long exponential tail which has been predicted in theoretical studies (Mangel & Tier, 1993; Lande et al., 2003). It is however notable that the initial population size in the experiment was n=4, which leads to an extremely strong influence of demographic stochasticity early on in the experiment. They also found higher extinction risks for populations under high environmental variation, measured as variation in food availability, compared to populations living under medium or low environmental variation. As mentioned earlier, the general theoretical prediction is that high environmental variation increases the risk of extinction (Lande, 1993), so Drake's result fits nicely into this framework.

A similar experiment was also performed by Belovsky et al. (1999; 2002), where they assessed the effect on brine shrimp (*Artemia franciscana*) extinction risk of initial population size, carrying capacity and the size of environmental variation. In line with theoretical predictions, lower environmental variation, greater initial population size and larger carrying capacity decrease extinction risk, but with smaller effects from initial population size than from the other two factors. Belovsky et al. (1999) also mention that "deterministic oscillations in population size due to inherent nonlinear dynamics and overcrowding" are as important, or more so, as the previously stated factors in determining extinction risk, which could suggest that density dependent effects is an essential part of this system. The importance of including density dependence in population models has been advocated by several authors (Boyce, 1992; Dennis & Taper, 1993; Sabo et al., 2004).

Schoener et al (2003) tested extinction models and predictions on an island system of two species of orb spiders. They used age structured models and observed extinction probabilities, and studied which model factors that were needed to obtain a good fit between predictions and observations. All three factors considered in their model, i.e. environmental stochasticity, demographic stochasticity and population ceiling were needed to explain the observed probabilities. The age structured model was also deemed superior to an unstructured counterpart. Schoener et al. therefore conclude that stochastic factors play a large role in empirical extinctions and that, at least for quantitative predictions, inclusion of extinction factors and life history traits is preferable to simplification.

Not a test of theoretical predictions concerning extinction risk, but rather an attempt to test stochastic population models in the form of PVA predictions was performed by Brook et al. (2000). They assembled data sets for 21 populations and split them in half, using the first part for parameterisation and the second part for evaluation. In their test they used five generic PVA packages, and tested whether the proportion of actual declines below threshold levels matched the predictions of the PVA software. The correlations between predictions and realized risk was generally fairly high (r^2 between 0.63 – 0.94), and without bias, so Brook et al. (2000) concluded that PVA is a valid and accurate tool for categorizing and managing endangered species. That study has subsequently been strongly criticised (Coulson et al., 2001; Ellner et al., 2002), with authors emphasising the lack of a power analysis, the lack of confidence intervals for the extinction risk estimates, and the fact that Brook et al. (2000) is comparing the average extinction risk over an ensemble of species.

Applying stochastic population models in conservation

The previous pages have hopefully hinted on the uses of stochastic population models in the practical conservation of species. There are a number of overlapping uses that span the area between basic and applied questions, where population models have a place to fill. Boyce (1992), Beissinger & Westphal (1998) and Beissinger & McCullough (2001) review Population viability analyses (PVA), and highlight stochastic models as a way to gain deeper

understanding on which processes have lead to species declines and how these declines can be reversed. However they caution the use of complex models that cannot be supported by quality data, as does Ludwig (1999) and Coulson et al. (2001). Since the risk of extinction in absolute terms is very sensitive to the parameters in a model and the model structure, the general advice is to mainly use PVA's for qualitative comparisons between management scenarios or to prioritize between populations for conservation, instead of using the quantitative results as absolute estimates of population extinction risk (Beissinger & Westphal, 1998). Some authors argue that due to parameter and model uncertainty, reliable predictions of extinction risks can only be made for time periods approximately 10-20% of the period used to estimate model parameters (Fieberg & Ellner, 2000). PVAs can however be used to obtain absolute estimates of risk, but these results must be interpreted with caution. The use of PVA methods in the International Red List in criterion E (IUCN, 2006), aims precisely at absolute estimates of risk. Many authors have also questioned the development of complex models, at least as a first step, since understanding of deterministic processes and knowledge of the overall population growth rate is of huge importance for a population's risk of extinction (Caughley, 1994). To perform a PVA you can either build a custom model, or use one of the many canned software that are available, e.g. RAMAS (Akçakaya, 1998), VORTEX (Lacy et al., 1995; Lacy, 2000) and ALEX (Possingham & Davies, 1995). Either way, it is important to know exactly what assumptions the model makes, and to check that these are reasonable, given the system. Beside strict PVA models, stochastic models can be used to assess populations in a more general way, e.g. how different management options will affect the population or which life-history stages are most important for population growth or extinction risk (Caswell, 2001).

Other uses of stochastic population models can be more general, and not geared towards the conservation of a certain population or species, e.g. as in trying to find patterns between population traits and extinction risk. These are the types of models covered mostly in this essay, and also the ones that aim toward general theory as opposed to specific applications.

Concluding remarks

Populations are subject to one final stochastic factor, which I have not mentioned so far in this essay, and that is genetic stochasticity. Genetic stochasticity is similar to demographic stochasticity since its effects also depend on the discreteness of individuals. The main stochastic processes that are connected to genetics are genetic drift and founder effect. Genetic drift can be defined as changes in allele frequency caused by the inherent randomness in births and deaths. This means that allele frequencies evolve by chance, and not mediated by selective advantages (Futuyma, 1998). This can result in fixation of (deleterious) alleles and nonadaptive evolution, both of which can be detrimental to populations and increase population extinction risk.

The founder effect is connected to colonization, and is the result of the randomness inherent in the genetic composition of the founder population. If the individuals founding a new population are few, the genetic composition of the new population can deviate substantially from the founding population (Futuyma, 1998). The impact of founder effects on extinction risk is hard to predict, and it can have both very negative and very positive effects on the persistence of the newly founded population, depending on the genetic composition of the founded population and how this interacts with the biotic and abiotic conditions in the new site. The direct result is however random change in the genetic composition of the founded population compared to the founding population, and this can lead to fixation, changes in allele frequency and (most likely) a decrease in genetic variation. Frankham (2005) argues

that most populations are not driven to extinction before genetic factors have a chance to act, so they must be seriously considered in models of population extinction.

Positive feedback loops between demographic stochasticity and genetic factors such as inbreeding and genetic drift cause these factors to reinforce each other. Such feedback loops have been termed the 'extinction vortex' (Gilpin & Soulé, 1986), here exemplified by the growth-vortex and the inbreeding-vortex, and can lead to continuous population deterioration. There is convincing logical arguments surrounding the concept of extinction vortices, but their relative importance and commonness in actual extinctions needs to be established (Fagan & Holmes, 2006). Another source of variation, briefly mentioned above, that also affect population viability is spatial heterogeneity. With stochastic temporal variation in the environmental conditions, spatial variation generally decreases the risk of extinction, compared to a static landscape (White, 2000). This is because bad years at some locations, with possibly local extinctions, are balanced by better conditions elsewhere. Assuming migration, the locally depleted or extinct populations can be recolonized from surviving populations, which decrease the risk of total population extinction (Hanski, 1999). The effect of spatial heterogeneity depends on many factors though, such as migration, spatial autocorrelation and isolation (Hanski, 1999; Ferrière et al., 2004).

 Environments are random and population numbers are discrete. Add to this the unpredictability of genetic drift, and the random component of spatial variation, and it should be very clear that stochastic population models are an essential tool to analyse populations. This essay have touched upon many aspects of stochastic population models, and has still only brushed the surface of what is possible, and sometimes reasonable, to include in a population model. It might seem impossible to consider all possible aspects, not least from the perspective of available data, and that the modelling exercise itself is therefore futile. However models should never model reality, only the most important aspects of it, and there can still be important lessons to learn from modelling specific systems. There is yet a gap between theoretical models of extinction and empirical validation of the relative importance of factors causing extinction. The number of studies that try to tease apart the contributions to extinctions from environmental and demographical stochasticity are still few (see above), and then factors such as genetics, spatial configuration and density dependence still remain. You can also question how far it is possible to proceed with general statements. The general patterns we can hope to find will surely be riddled with conditional statements that constrict their scope and influence. To continue exploring this space of interactions between life history, variation and randomness is however of paramount importance to further ecological understanding and to guide species conservation.

Acknowledgements

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