Extinction Risk in Fluctuating and Heterogeneous Environments

by

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for the degree of Master of Science in Mathematics in the
Faculty of Science at Stellenbosch University*

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Declaration

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Date: .... December 2019

Abstract

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We model the effects of demographic and environmental stochasticity in the logistic, Gompertz and Ricker models. We focus on factors affecting extinction risk in a lone population as well as in pairs of competing populations. A thorough numerical analysis of extinction probability is given. We find that colored environmental noise causes reductions in extinction risk, and that correlation between the environmental noise experienced by two competing populations increases extinction risk. The Ricker model exhibits a high rate of persistence in comparison with the logistic and Gompertz models.

Uittreksel

Uitwissing Risiko in Wisselende en Heterogene Omgewings

("Extinction Risk in Fluctuating and Heterogeneous Environments")

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Tesis: MSc

Desember 2019

Ons hoofdoelwit is om die bevolkingsdinamika in veranderlike omgewing te bestudeer. Ons beskou demografiese en omgewingsstogastisiteit in die logistieke, Gompertz- en Ricker modelle. Ons ondersoek die dinamiek van 'n enkele bevolking en kompetisie in tweebevolkings modelle. 'n Deeglike numeriese analise van uitwissing waarskynlikheide word gegee. Ons toon aan dat die Ricker-model 'n hoë tempo van voortbestaan toon in vergelyking met die logistieke en Gompertz-modelle. Ons verken 'n reeks parameters deur die simulasies.

Acknowledgements

I would like to thank my advisors Professor Cang Hui and Dr Pietro Landi for their guidance and help through all this work.

Dedications

To my beloved mother, may Allah shower her with blessings!

Contents

CONTENTS **vii**

List of Figures

List of Tables

Chapter 1

Introduction

1.1 History

Over the last two centuries, ecologists have developed a plethora of models and techniques in order to better understand population dynamics. We begin with a brief overview of some of the key moments in this history. The exponential growth model, introduced by Robert Malthus [59], was one of the first models to study population dynamics, and has since been extensively studied by many ecologists and applied mathematicians [2, 6, 28].

A short while later, Pierre François Verhulst [83] published the logistic population growth model. In the Verhulst model, population growth follows a sigmoid curve shape, with initially fast (exponential) growth, slowing down over time as the population approaches a 'carrying capacity' defined by the environmental conditions. This introduced the concept of density-dependent population models; since then many different model formalizations have been defined, such as the Ricker and Gompertz models [24, 72].

Alfred James Lotka [53] developed two differential equations to describe a prey-predator interaction. Independently from Lotka. Vito Volterra also developed an equivalent model describing the relationship between two species. The Lotka-Volterra model can be used to explore various *types* of interspecific relationships such as competition, mutualism, predation, and parasitism. Since then, numerous studies have extended these models to address a variety of problems [2, 8, 56].

Ecologists began to question their studies and findings for more clarity and improvement, searching for realistic and convenient models. While the

models just mentioned all have applicability to ecosystem stability, the subject received increasing attention around the time that Robert May published his ground-breaking paper relating the stability of an ecosystem to its complexity [61]. Not long after, a model was published incorporating the effects of random environmental fluctuations on the stability theorem [13, 14].

The study of stochastic population dynamics started in 1949, with David G. Kendall [39] who studied the stochastic fluctuations in age distributions. This was followed by several studies of random environmental variation looking at how this randomness affects the fate of local residents and how this will extend to affect the global ecosystem [49, 73]. Furthermore, in extending these studies new concepts and approaches emerged such as the minimum viable population, quasi-extinction level, and population viability analysis (PVA) [23, 71, 76].

1.2 Why use population models?

Population models are a transformation of real dynamics to the forms of mathematical models, and their purpose is to study population dynamics. Mathematical models allow their users to gain a better understanding in order to answer many important questions such as: how does a population grow, interact and disperse? What makes some populations persist when others go extinct? What underpins ecosystem stability and facilitates species coexistence? Models are useful for addressing and directing the study of interactions within and between population and environments, such as density-dependence, competition, and seasonal dynamics. Models are widely used in decision-making around the management of ecological resources. Modeling interactions makes it possible to identify valuable patterns and trends in population dynamics.

Population models are used in the study of endangered populations and agricultural management. Common examples include determining what conditions allow for a maximum harvest, avoiding biological invasions from unwanted populations (including diseases), and protecting and endangered species or ecosystem [1, 18, 19].

1.3   Study objectives and research questions

One of the major problems in ecological studies is how to estimate the probability of extinction for any population. The persistence or coexistence of a population or community is affected by its structure as well as the environment(s) in which it lives, e.g. population (or community) size, diversity, environmental stochasticity, the quality and strength of interactions within and between species, etc [12, 44, 58].

Sustained species persist and coexist as a consequence of stabilizing mechanisms. Stabilizing mechanisms vary widely and include fluctuation independent as well as fluctuation dependent mechanisms. For instance, rare prey species experience some protection due to their low rates of encounters with the predators (or competitors), and environmental variations affect each population differently in each season [10]. The persistence or the stability of any population depends on several factors, including the population growth rate, the magnitude of the environmental or demographic stochasticity, the rate of recovery from low species density, and many others [12].

In general, in studying the stability of an ecological populations, analytic as well as numerical tools are used, for example when applying qualitative stability analysis to deterministic models. In this research, we use stochastic models to study the persistence, coexistence, stability, and extinction of the species population. We focus on the following questions:

1. How does the position in each model of incorporated environmental noise (added either to the growth rate, carrying capacity, or directly to the model) affect the model's predictions for species persistence?

2. How does temporal autocorrelation in the environmental stochasticity (coloured noise) affect the population dynamics, persistence and species coexistence?

3. What effects do the levels of environmental variance and demographic variation have on the persistence and extinction rates predicted by each model?

These question are explored using both single-population models and competitive two-population models.

1.4   Thesis overview

We begin in Chapter 2 with a brief overview of the three density-dependent models we utilise in the rest of this work. In Chapter 3, we study the stochastic dynamics of a single species, with environmental and/or demographic stochasticity. We incorporate stochasticity into the three models in various ways, adding environmental noise to different parts of each model. We explore the effects of environmental noise variance, environmental noise autocorrelation, and demographic stochasticity with a range of demographic growth parameter values. We compare the effects of these various assumptions on quasi-extinction and extinction probabilities using numerical simulations.

In Chapter 4, we study the persistence and coexistence of two competing species using variants of the stochastic logistic, Gompertz and Ricker models. We again examine the effects of noise variance, autocorrelation, position in the model, etc., and in addition explore the effects of different correlation levels between the environmental noise effects experienced by the each of the two species.

In our study, we focus on the use of numerical simulations, supplemented at times with theoretical analyses and statistical approaches. We utilise three different models, characterising the effects of a wide range of assumptions regarding the role of environmental noise and demographic stochasticity in the dynamics of population extinctions.

Chapter 2

Population Models in Discrete Time

In this chapter, we give a short description of the deterministic single population models which form the basis for the models used in Chapters 3-5.

2.1 Logistic model

In the logistic model, the size of the population is regulated by its "carrying capacity". This stands in contrast with exponential growth model, where populations grow without limit: this would be very unusual to happen in nature. The logistic model is introduced by Pierre-François Verhulst [83] where the population growth is proportional to the population size and the resource availability. The self-regulating growth-per-timestep can be described by the following equation:

$$N_{t+1} - N_t = \lambda N_t (1 - \frac{N_t}{k}),$$ (2.1)

where N_t is the population size, λ represents the growth rate (including reproduction as well as death/survival) and k is the carrying capacity. If $N_t = k$ then $N_{t+1} = 0$.

2.2 Ricker model

W. Ricker [72] introduced his discrete time model to describe the dynamical population growth of cannibalistic fish for the purpose of fishery stock man-

agement, though it has since been used as base for a variety of modelling applications [4, 30, 50]. In the Ricker model the population size at time step $t + 1$, base on the population at time t, is given by:

$$N_{t+1} = N_t e^{\lambda(1-\frac{N_t}{k})}, \tag{2.2}$$

where N_t is the population size, λ represents the growth rate, and k is the population carrying capacity. If $N_t = k$ then $N_{t+1} = 0$.

2.3 Gompertz model

The Gompertz model is introduced by Benjamin Gompertz [24]. It has been studied extensively in contexts of industrial ecology such as cell line production and commercial agriculture, as well as in medical contexts as a model for tumor growth [22, 80, 89]. In the Gompertz model, the population size at time $t + 1$ is given by:

$$N_{t+1} - N_t = \lambda N_t \log(\frac{k}{N_t}), \tag{2.3}$$

where N_t is the population size at time t, λ is the population growth rate, and k is the carrying capacity.

(a)
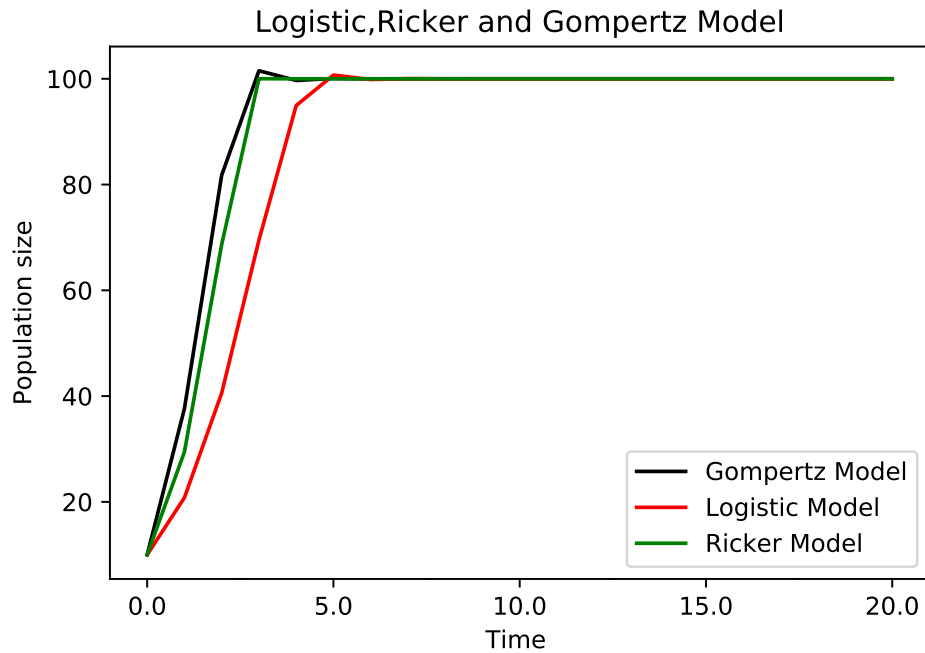
Figure 2.1 – Sample trajectories of the deterministic logistic, Ricker and Gompertz models. Initial population size $N_0 = 10$, intrinsic growth rate $\lambda = 1.2$ and carrying capacity $k = 100$.

Figure 2.1 shows deterministic growth in the logistic, Ricker and Gompertz models. We observe that the logistic model (red curve) exhibits the slowest overall growth and Gompertz model (black curve) exhibits the fastest growth. We plot N_t against N_{t+1} (Figure 2.2) as a reference point for our analyses. The most clear difference between the models is how they respond to large population sizes: clearly the Ricker model is much more forgiving to overpopulation, which causes extinction much more easily in the Gompertz and logistic models.

(a)
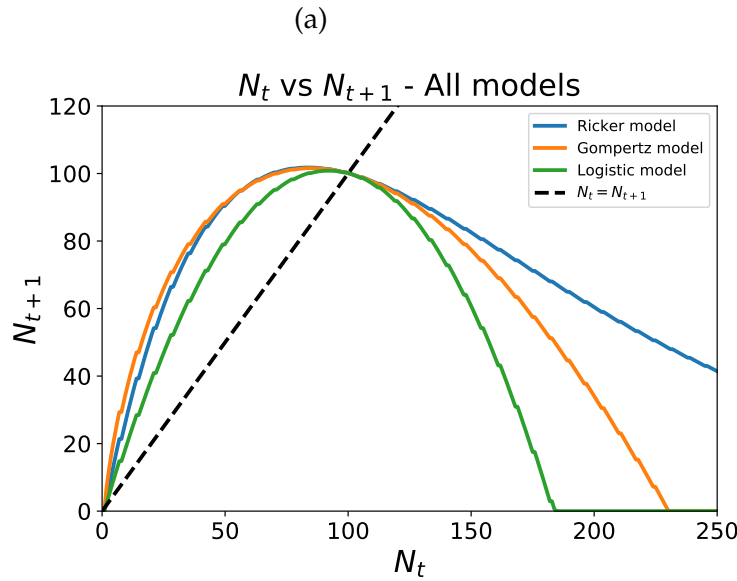
Figure 2.2 – Plot of N_t against N_{t+1} for the deterministic logistic, Ricker and Gompertz models with intrinsic growth rate $\lambda = 1.2$ and carrying capacity $k = 100$.

2.4 Growth rate

The population growth depends on the sum of each individual's performance. Here we characterise the demographic growth parameters λ for each model in terms of the population sizes for two consecutive years. In the logistic model, the demographic growth parameter for year t is given by:

$$\lambda = \frac{k(N_{t+1} - N_t)}{N_t(k - N_t)}. \tag{2.4}$$

For the Ricker model, the demographic growth parameter is given by:

$$\lambda = \frac{k \ln(N_{t+1})}{(k - N_t) \ln(N_t)}. \tag{2.5}$$

For Gompertz model, the demographic growth parameter is given by:

$$\lambda = \frac{N_{t+1} - N_t}{N_t \ln\left(\dfrac{k}{N_t}\right)}. \tag{2.6}$$

Chapter 3

Stochasticity in single-population models

3.1 Introduction

Organisms interact with and depend on their environments. These environments vary in both random and predictable ways, and such variations affect the dynamics of resident populations. Various aspects of the system dynamics exhibit noisy characteristics, and may be broadly categorised into variations in the number of birth and death events from one individual to another ("demographic stochasticity"), and variations in the average reproductive (growth) rate from season to season ("environmental noise") [42]. Variations in birth and death rates may depend on factors such as population size, age structure or the number of females in the population. Between successive time steps (seasons), the magnitude of the environmental variation could be large or small. The presence of variation motivates us to consider both the deterministic and the stochastic elements when analysing population models [43].

In modeling and analysing real population dynamics from collected data, the magnitude of the random variations is often augmented by the observation (measurement) error, or by taking small sample sizes, therefore, it will effect the analysis outcome [82]. In early attempts to predict changes in population sizes, scientists used deterministic models; such models produce point estimates for future populations based on an initial population and use predefined environmental and demographic parameter values. Real en-

vironments are however varying randomly, and every individual organism is unique. Attempts to capture these variable and not-fully-predictable elements of the real world inspired the field of stochastic population modeling. Stochastic models estimate the probability distributions for potential outcomes of a system over time, they are widely used to analyse temporal changes in the population dynamics. Stochastic models allow us to apply different kinds of analysis that deterministic models do not allow. For example, using stochastic models we are able to estimate the probability distributions of possible population size, or extinction probabilities for various future times [34, 42, 29]. Source of stochasticity that contribute to the dynamics of any population may be categorised into three groups: demographic stochasticity, environmental stochasticity and estimated error stochasticity [43].

With variety of stochastic continuous models analysis, the stochastic discrete models has been received very much less attraction, because of the difficulties of analysing the models even without the adding any stochastic term (for example, chaotic behaviour and bifurcation theory) [55, 92].

3.2 Outline

In this chapter, we study the effects of stochasticity in logistic, Ricker and Gompertz models. We simulate these three models with demographic and different white and coloured environmental noise (pink and red). We explored the effects of these forms of noise on the probability distributions of persistence and extinction risk, the average population size and its variance. In the following sections, we present the analytical and theoretical background for evaluating stochastic population dynamics using these different models. We then examine the effects of adding demographic and environmental noise on the dynamics of logistic, Ricker and Gompertz models, and compare the results. Individual fitness values are sampled from Poisson distributions (demographic stochasticity), while environmental noise is generated via a normal distribution, using different processes to obtain white, pink and red noise.

3.3 Models description

In this section we are going to give short description of the models, we developed these models with different types of stochasticity and noise to address the potential impact of changes and noises.

3.3.1 Demographic stochasticity

Demographic stochasticity drives fluctuations in birth and death rates caused by individual variability as well as population social and spatial structure. We define demographic stochasticity as the variation in the number of offspring produced per individual in the population [43]. The discrete events of birth and death happen on a random (probabilistic) basis so that, for instance, in our analysis repeating any simulation with the same initial values will lead to different outcomes. While if the individuals in the population are identical they will have the same probability of the birth and death, there will still be demographic stochasticity in the average population growth. There are two major sources of demographic stochasticity:

- Within-individual scale reflects the probabilistic nature of birth and death events.

- Between-individual scale reflects the fact that each individual has a different probability distribution of birth and death events due for example to variations in genotype and body size.

3.3.1.1 The demographic assumptions

We model populations of asexual individuals which reproduce annually.

- Every year, each individual either dies, survives without reproducing, or survives and reproduces $(0 \leftarrow 1, 1 \leftarrow 1, 2+ \leftarrow 1)$.

- The total fitness of the population at time t is made up of contributions from each individual at that time; we represent this as f_i which is a contribution from the individual i. We used Poisson distribution to sample individual fitnesses. Therefore, the total population fitness is given by,

$$\mathbb{F} = \sum_{i=1}^{n} f_i, \tag{3.1}$$

- To model population dynamics, we use the average growth rate. In this case, the mean population fitness is given by the average (stochastic) growth rate λ_t

$$\lambda_t = \overline{\mathbb{F}} = \frac{1}{n}\sum_{i=1}^{n} f_i. \tag{3.2}$$

3.3.1.2 Demographic variance

Future generations depend on the reproductive success (fitness) of individuals from previous generations. Part of the unpredictability/variability of future population sizes comes from the variability in individual fitnesses. Demographic variance is defined as the variance in individual fitness, and it is given by,

$$\sigma_d^2 = \frac{Var(\Delta N_t)}{N_t}, \tag{3.3}$$

Where, ΔN_t is the rate of change in the population size N_t, σ_d^2 is the demographic variance.

3.3.2 Environmental stochasticity

Random fluctuations in environmental conditions influence average birth and death rates of resident populations. Environmental stochasticity refers to unpredictable spatial and temporal fluctuations in environmental conditions; for the purposes of population modelling we may restrict our definition to the *effect* that such fluctuations have on the residents. Environmental stochasticity influences how population sizes fluctuate and affects the fate of populations. In other words, environmental stochasticity, which is a basic feature of any natural system, may be represented as variations in the parameters influencing population growth from year to year.

For many years, the environmental noise has been modeled using a white spectrum that influences the population dynamics. There are however numerous studies suggesting that most environmental noise is in practice not white, but instead is usually correlated [77] (pink or red) noise; i.e. the environmental condition for next year is more likely to be same as the previous year. Recent studies have emerged which utilise coloured noise spectra [29, 34, 35]. The assumption of a white spectrum is generally thought to be an unrealistic choice for representing the noise in many population studies,

so in order to present more realistic models, we have moved beyond the scope of the white spectrum.

Multiple existing studies examining the effects of environmental variation used white noise to generate this variation, so that there is no temporal autocorrelation in the environmental fluctuations [69]. A more recent study analyses time series data of population dynamics while gradually increasing in the magnitude of the temporal autocorrelation [25, 63].

Noise spectra may be referred to by the level of temporal correlation in time series data they generate; equivalently, a noise spectrum may be characterised by the relationship between frequency and "power spectral density PSD" which it exhibits. The power spectral density describes the distribution of power into frequency components. Time series data is said to be white when there is no dominant frequency (uniform power spectral density). Low frequencies dominate the time series data of pink and red noise, while high frequencies dominate the time series data of blue noise [54].

The power spectral densities of pink noise fluctuations are inversely proportional to their frequencies ($\frac{1}{f}$) [31, 36, 79], while those of red noise fluctuations are inversely proportional to their frequencies squared ($\frac{1}{f^2}$) [37, 79]. The population dynamics could be represented by the difference equation:

$$N_{t+1} = N_t F(\tilde{\lambda}_t, N_t). \tag{3.4}$$

There are at least three different ways to incorporate the environmental stochasticity into models of population dynamics. We can add the environmental noise 'to the model' directly, to the growth rate, or to the carrying capacity. For example, the logistic model with the environmental noise influence in the model, growth rate and carrying capacity will set

$$N_{t+1} = \tilde{\lambda}_t N_t (1 - \frac{N_t}{k_t}) + S_t, \tag{3.5}$$

where N_t is the population size, S_t the environmental noise, $\tilde{\lambda}_t = \lambda_t + S_t$ is growth rate with both demographic and environmental stochasticity and k_t is the carrying capacity with environmental noise ($k_t = k + S_t$). When we add environmental noise into the Ricker model we have:

$$N_{t+1} = N_t e^{\tilde{\lambda}_t(1 - \frac{N_t}{k_t})} + S_t, \tag{3.6}$$

Finally, when we add environmental noise into the Gompertz model we have:

$$N_{t+1} = \tilde{\lambda}_t N_t Log(\frac{k_t}{N_t}) + S_t, \tag{3.7}$$

Note that, in the model, the environmental noise is included in one position only.

In our analysis, we utilise various types of noise, generated using modified normal distributions. The aim of this section is to explore different placements of environmental noise in the three models. We want to find out: where does environmental stochasticity most influence population dynamics.

3.3.2.1 White, pink and red noise

White, pink and red noise distributions are used extensively in stochastic population models to represent environmental fluctuations. White noise is a term used to describe uncorrelated random time series signals, with zero mean and constant variance. The points in white noise time series are independent (i.e. uncorrelated) and the signal power, also called "power spectral density (PSD)", is equally distributed between frequencies. In other words, white noise time series have, on average, equal energy in every equally-sized frequency interval.

Noise may be more generally characterised by its power spectral density. In this work, we consider power-law noise, with spectral densities of the form $S(f) \propto \frac{1}{f^{\beta}}$. The exponent β in the power spectral density describes how power is distributed among frequencies in the noise; for white noise, $\beta = 0$ and the power spectral density (PSD) is flat.

"Pink" and "red" describe noise signals for which $\beta = 1$ and $\beta = 2$ respectively, and as such are often referred to as $\frac{1}{f}$ and $\frac{1}{f^2}$ noise. Such noise signals have non-zero autocorrelation, and their power decreases as the frequency increases. As a result, the lower frequencies are dominant in pink noise, and even more so in red noise. Pink and red noise series may be obtained by filtering white noise, to reduce the presence of high frequencies. The most well-known way to generate red noise is the autoregressive process [82]; there are several processes with which one may generate pink noise, such as recurrence models, non-linear stochastic differential equations, Fourier transformation and wavelets [31, 36, 37, 38, 75, 79]. Based on Timmer and

Koenig algorithm [79], we generated each $\frac{1}{f^\beta}$ spectrum using Python program. We tested the autocorrelation and PSD of the samples generated in order to validate the algorithm's implementation.

Timmer and Koenig's algorithm generates power-law noise by first generating a Fourier transform with randomised amplitude and phase, then performing an inverse Fourier transform to obtain data in the time domain - the power-law noise [79].
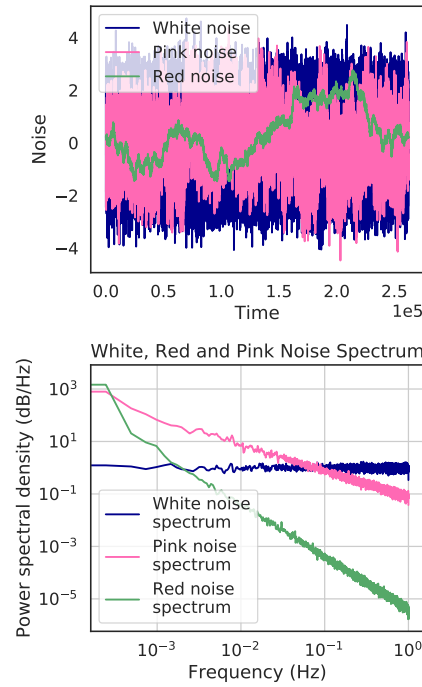
Figure 3.1 – Red, pink and white noise samples. (Above) Time series illustrate varying levels of autocorrelation. (Below) Power spectral densities of the three time series.

3.3.2.2 Variance σ^2, autocorrelation ρ and Beta β

The variance σ^2 refers to the spread of the time series data, i.e., how far their width is from the mean. Variance is particularly useful in predicting the future states or the performance of the any population dynamics [68, 88]. Autocorrelation ρ is the degree of similarity in the time series data over the successive time interval. It is the same as calculating the correlation between two different time series, except that the same time series is actually used twice. Correlation is a statistical technique that can show whether and

how strongly pairs of variables are related [41, 74]. Beta β is the PSD exponent which describes how the power is distributed among frequencies in the noise.

The differences between white, pink and red noise can also be described in terms of σ^2, ρ and β [82, 37] - we summarise the properties of these three noise colours below:

- White noise has constant σ^2, $\rho = 0$ and $\beta = 0$.

- Pink noise has increasing σ^2 ($\propto \log(t)$), $0 < \rho < 1$ and $\beta = 1$.

- Red noise has increasing σ^2 ($\propto t$), $0 < \rho < 1$ and $\beta = 2$.

In this work, we explore the effects of a variety of environmental noise types: white noise with variances $\sigma^2 \in [0, 30]$, noise with unit variance and $\beta \in [-1, 5]$

Exploring the effects of different types of environmental noise, with different parameter values, is a long process. In this work we consider the following scenarios:

- White environmental noise with $\sigma^2 \in [0, 30]$.

- Noise with unit variance and $\beta \in [-1, 5]$.

- Pink and red noise with unit variance and autocorrelation $\rho = 0.85$ and $\rho = 0.9$ respectively.

3.4 Simulations

We simulated time series of population dynamics according to the stochastic logistic, Ricker and Gompertz model, which are useful in many conservation biology applications. We consider fluctuations in the environment affecting the annual population growth, where, N_t is the population size in year t, with λ_t as the demographic growth rate at year t. We repeated those simulations with only demographic stochasticity, then with only environmental noise S_t in different positions and finally with both demographic and environmental stochasticity to capture the dynamics.

The noise S_t that was added as the environmental fluctuations factor can be white, pink, or red, in order to see weather the different colours of noise in

different positions will affect population growth differently. We simulated population dynamics for 20 "years" in environments, the initial population size is 10 and the carrying capacity is set to 100. The variance of the environmental noise is 1 and with zero mean (white, pink and red); the autocorrelation in the pink and red noise time series is .85 and .9 respectively. We simulated the demographic growth λ_t using a Poisson distribution with mean 1.2.

3.4.1 Demographic noise

In this section we model the effects of the demographic stochasticity. Individual fitness values are sampled from a Poisson distribution; the mean fitness value provides the contribution of demographic stochasticity to the average growth rate λ_t. The initial conditions implemented for the simulation of all three models are: initial population size is 10, the individual fitness values are sampled from a Poisson distribution with mean $\lambda = 1.2$ and the carrying capacity is set to 100.

(a)
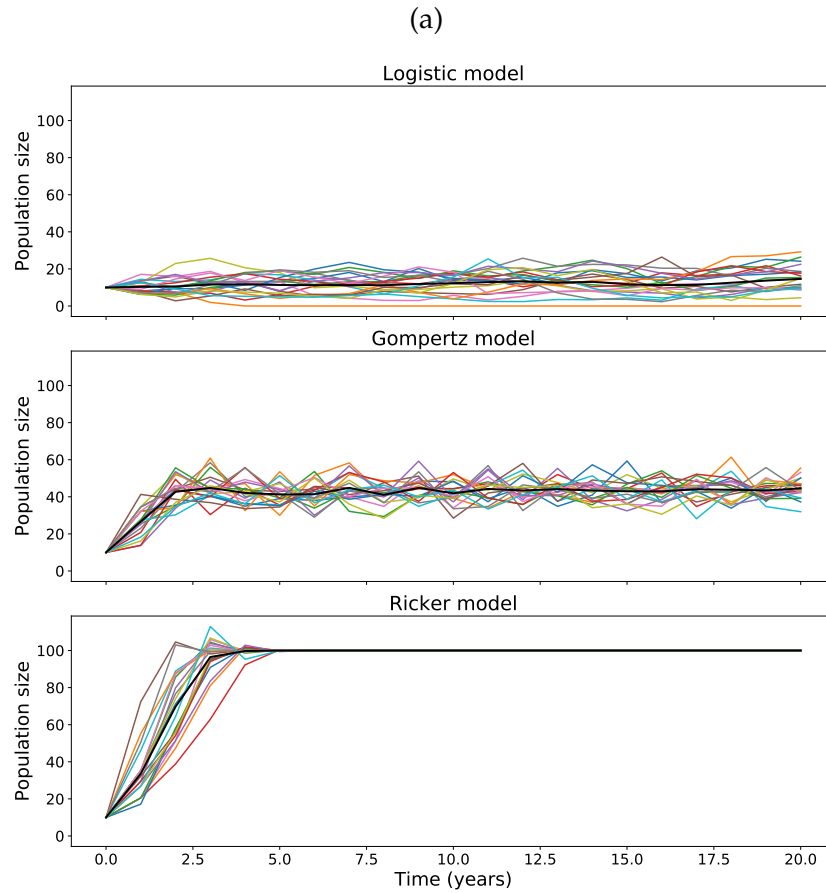
Figure 3.2 – Sample trajectories of the Logistic, Gompertz and Ricker models with demographic stochasticity included in the growth rate. Initial population $N_0 = 10$, carrying capacity $k = 100$ and each individual's reproductive success is sampled from a Poisson distribution with $\lambda = 1.2$.

We calculated the average growth and the variance of each model. Each trajectory has growth rate (λ_t) at time t. The trajectory j has λ_{t_j} growth rate at time t. μ the average of λ_{t_j} across j, i.e. we took the average of all the simulation in yearly bases, the we calculated the variance of this averages. As expected from the deterministic model, the stochastic logistic model exhibits much slower average growth than the Gompertz and Ricker models. Surprisingly however, the average growth rate in the stochastic Ricker model is higher than in the stochastic Gompertz model as shown in Figure: 3.3, the plot of the expected N_{t+1} against N_t. Clearly, in this version of the logistic model and with only demographic stochasticity, the population cannot reach the value of the "carrying capacity" parameter (100), but instead forms its own carrying capacity.

(a)

(b)

(c)
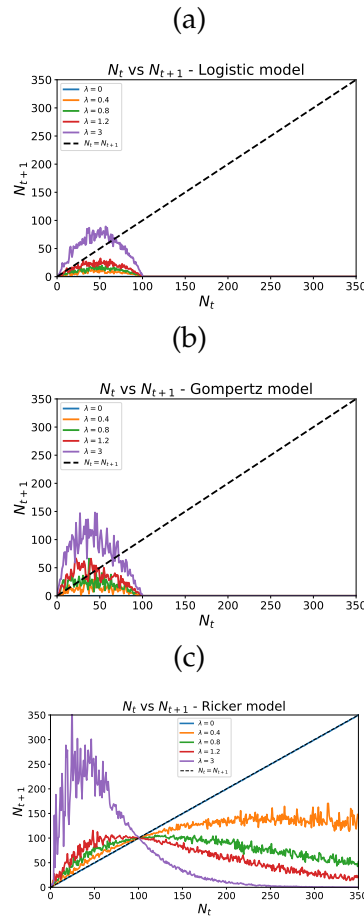
Figure 3.3 – Sample trajectories of N_t and N_{t+1} of the logistic, Gompertz and Ricker models with demographic stochasticity included in the growth rate, with different Poisson mean parameter. Initial population $N_0 = 10$, carrying capacity $k = 100$.

Table 3.1 – The average growth rate μ and its variance σ^2 of the average trajectory from 20 trajectories; with demographic growth rate in the logistic, Gompertz and Ricker models (no environmental noise included). The demographic stochasticity is sampled from a Poisson distribution with $\lambda = 1.2$.

Model	μ	σ^2
Logistic model	0.1	0.07
Gompertz model	1	0.7
Ricker model	1.1	1.9

3.4.2 Environmental noise
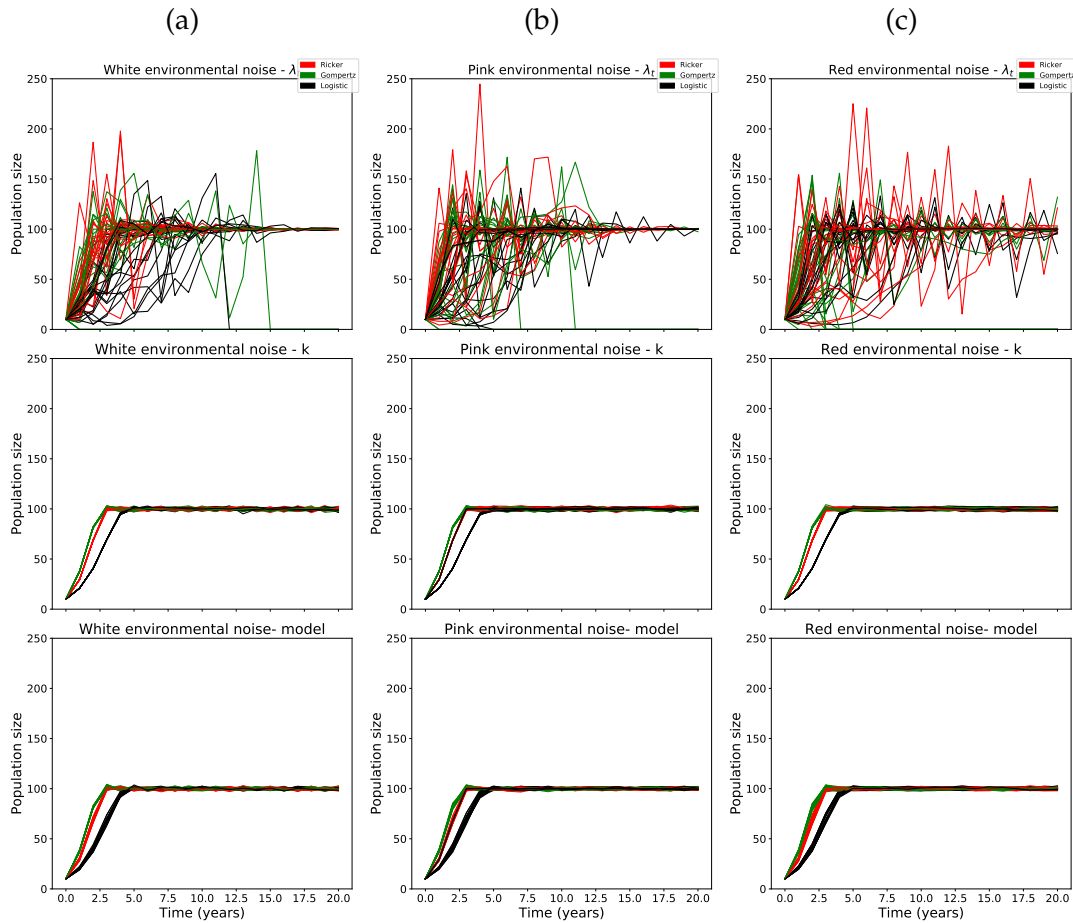
Figure 3.4 – Simulations of the logistic, Ricker and Gompertz models with white, pink and red environmental noise. In the first column, white (*a*) pink (*d*) and red (*g*) environmental noise is added to the growth rate λ; in the second column white (*b*) pink (*e*) and red (*h*) environmental noise is added to the model; in the third column white (*c*) pink (*f*) and red (*i*) environmental noise is added to the carrying capacity k. In all cases $N_0 = 10$, base carrying capacity $k = 100$ and simulations run for 20 years of reproduction. All three models are included in each of the figures.

In this section we model the effects of white, pink and red environmental noise in the population demographics. The average growth rate $\lambda = 1.2$. The variance of the environmental noise is 1 and with zero mean (white, pink and red); the autocorrelation in the pink and red noise time series is $\rho = 0.8$ and $\rho = 0.9$ respectively. We explore the respective effects of adding the environmental noise term to the growth rate λ, directly to the model or

to the carrying capacity *k*. The initial conditions implemented for the simulation of all three models are: initial population size is 10, and the carrying capacity is set to 100.

3.4.3   Demographic stochasticity with different colours of environmental noise

In this section we model the effects of white, pink and red environmental noise in the presence of demographic stochasticity. Individual fitness values are sampled from a Poisson distribution; the mean fitness value provides the contribution of demographic stochasticity to the average growth rate λ_t. We explore the respective effects of adding the environmental noise term to the growth rate, directly to the model or to the carrying capacity.

For instance, some ecologists consider the environmental variation to be mainly affecting the carrying capacity, and so add it to the carrying capacity. Others focus on the effect directly in the growth rate, while still others model environmental variations as random errors, so they just added random terms directly to the model at each time step. Here we consider all three cases, and we compare in how the population will grow with different models and different parameters configurations. There is autocorrelation in the pink and red noise, therefore, there is an environmental autocorrelation included in the models. Put simply, this means that the growth each year is likely to be similar to that in the previous year.

In all scenarios, we simulate trajectories for 20 years, and calculate the average trajectory of 100 model populations, focussing on the variance and the mean of this average trajectory. We set the initial population size to 10 and the base carrying capacity to 100. Individual fitness values are sampled from a Poisson distribution with $\lambda = 1.2$. The variance of the environmental noise is 1 and with zero mean (white, pink and red); the autocorrelation in the pink and red noise time series set to $\rho = 0.8$ and $\rho = 0.9$ respectively.
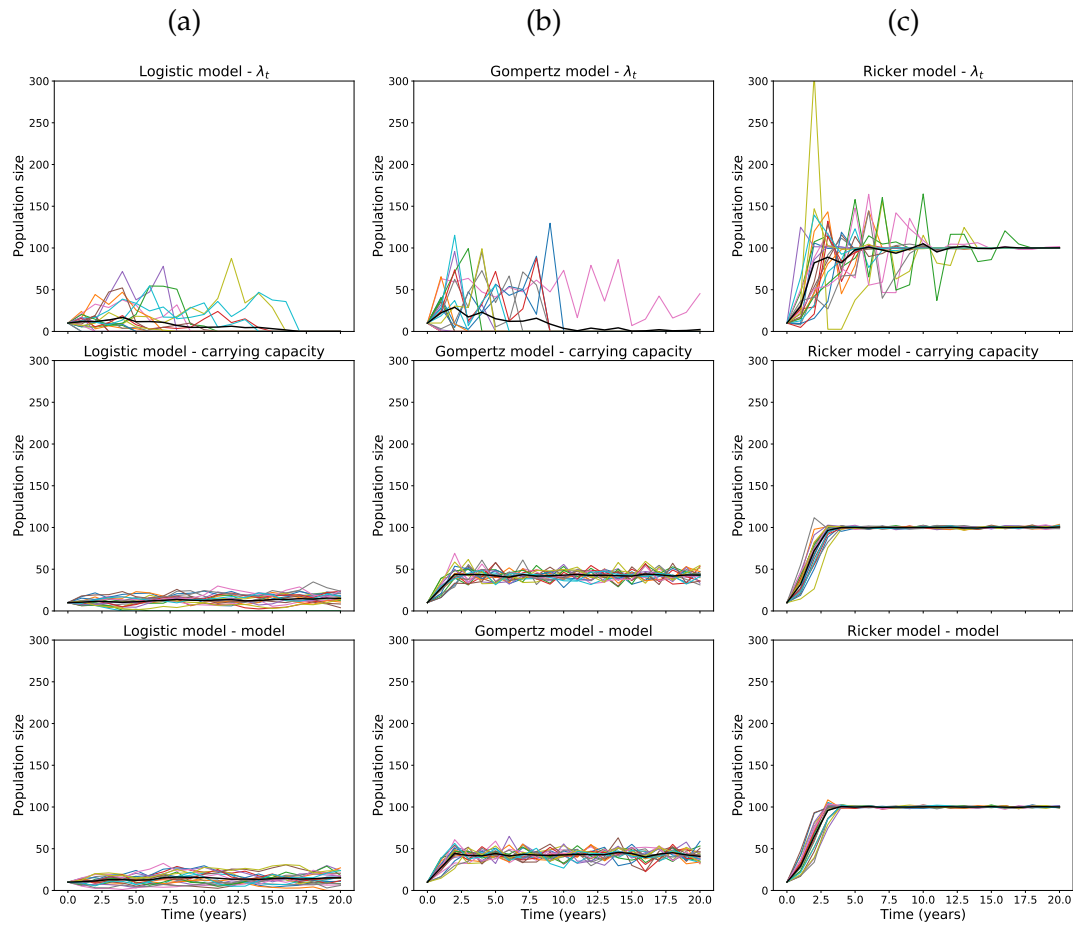
Figure 3.5 – Sample trajectories of the logistic, Ricker and Gompertz models with white environmental noise in different positions. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$ and simulations run for 20 years. The black line represents the average population size at each time-step.
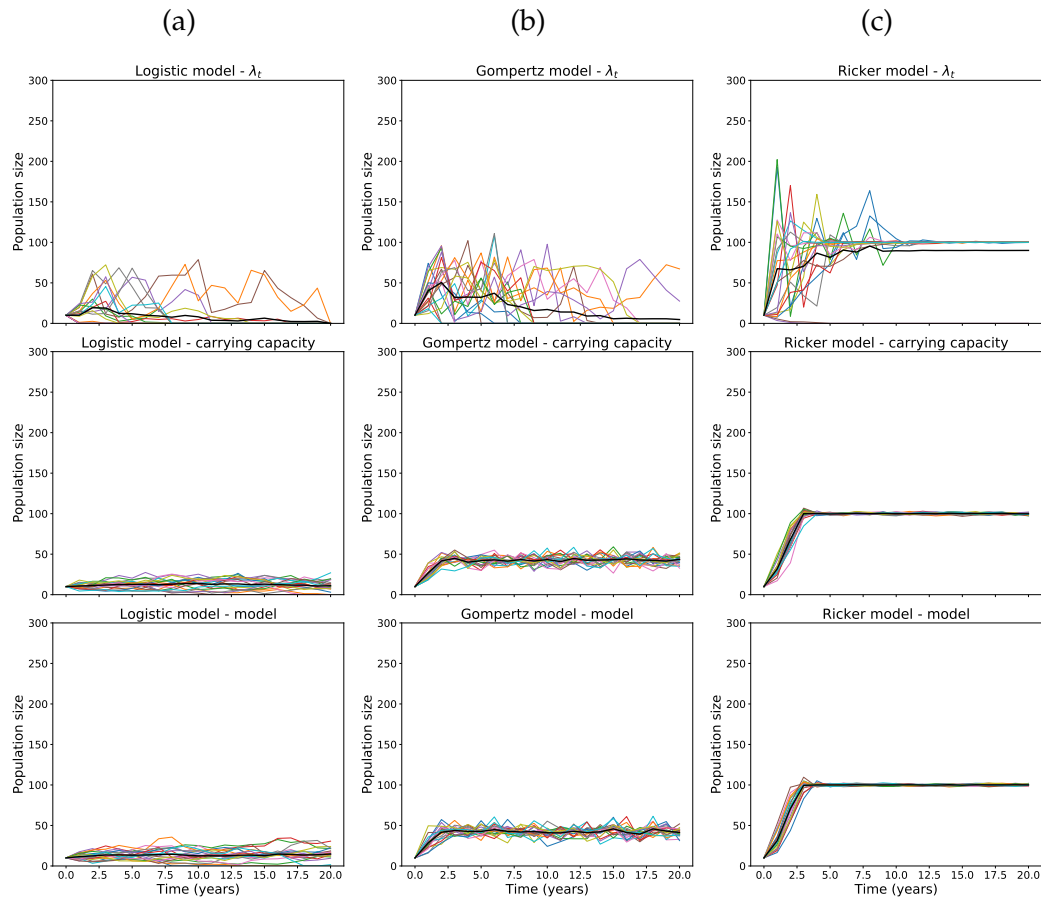
Figure 3.6 – Sample trajectories of the logistic, Ricker and Gompertz models with pink environmental noise in different positions. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$ and simulations run for 20 years. The black line represents the average population size at each time-step.
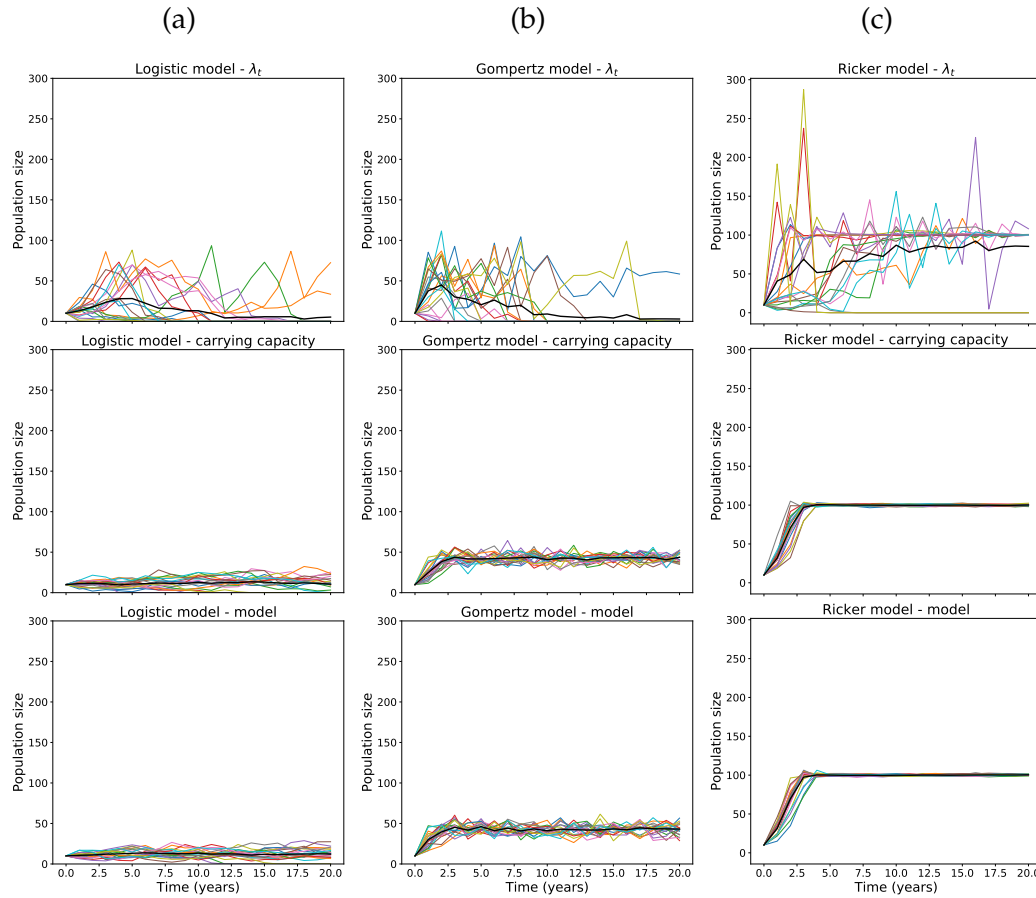
Figure 3.7 – Sample trajectories of the logistic, Ricker and Gompertz models with red environmental noise in different positions. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$ and simulations run for 20 years. The black line represents the average population size at each time-step.

Based on the above simulations, we notice the following:

- A common trend between all three models is that adding demographic and environmental stochasticity slows the growth and decreases the effective carrying capacity.

- In the presence of demographic stochasticity, the three models behave quite differently (Figure 3.2). Once the population has reached a stable level, the variance between population values in the logistic model is

much lower (0.07) than the variances observed with the Gompertz and Ricker models (0.7 and 1.9 respectively).

- Adding white, pink and red environmental noise (without demographic noise) to a constant growth rate (i.e. $\lambda + S_t$,) leads to large variability in the simulation trajectories. This causes extinction in some of the trajectories (this occurs mostly in the first few years) while others settle around the base carrying capacity (figure 3.4, first row). In comparison, when adding the noise to the carrying capacity (i.e. $k + S_t$) or to the model (i.e. $F(N_t, \lambda) + S_t$) populations grow more quickly and directly to their carrying capacity k (figure 3.4, second and third rows).

- The autocorrelation in pink and red noise causes more variability around the carrying capacity, with more autocorrelation having a stronger effect with red noise (figure 3.4).

- Including the white environmental noise in the growth rate and with the demographic stochasticity i.e. ($\tilde{\lambda}_t = \lambda_t + S_t$, Figure 3.5 - first row), the results is increasing in the average growth relative to the model with only demographic stochasticity (no environmental noise) shown in Tab: 3.1 and 3.2, also, the variance is relativity lower. The logistic model has the highest variance which explains why the trajectories vanished when we adding the noise into the λ_t. In case of adding the white noise to the k or to the model, the behaviour of each model were very similar Figures: 3.5-second and third row.

- In all the models, adding both demographic and pink environmental noise to the growth rate (Figure 3.6 - first row), results in decreasing the average growth relative to the model with white environmental noise (Figures 3.5 - first row), and also increases population variance is relativity higher.

- Adding pink noise into the carrying capacity or into the model directly results in average growth rates which are pretty similar to those obtained with white environmental noise (Figures 3.5).

- In simulations with demographic stochasticity adding red environmental noise into the growth rate (i.e. $\tilde{\lambda}_t = \lambda_t + S_t$, Figure 3.7), tend

Noise	White noise						Pink noise						Red noise					
Position	λ_t		Model		k		λ_t		Model		k		λ_t		Model		k	
Measure	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2	μ	σ^2
Logistic	0.1	0.6	1	0.1	1	0.1	0.5	0.06	1	0.09	1	0.1	0.04	0.4	1	0.1	1	0.09
Gompertz	0.1	0.6	1.1	0.8	1.1	0.7	0.3	1.6	1.1	0.7	1.1	0.6	0.03	1.06	1.1	0.8	1.1	0.7
Ricker	0.1	2.3	1.35	1.9	1.35	1.9	0.05	2	1.35	1.9	1.35	1.9	0.05	2.1	1.35	1.9	1.35	1.9

Table 3.2 – The variance and average growth of the average of the trajectories, with the effect of demographic and white environmental noise in the logistic, Ricker and Gompertz models. The demographic noise is sampled from Poisson distribution with $\lambda = 1.2$, and the white environmental sampled from a standard normal distribution $S_t \sim \mathcal{N}(0,1)$. Without environmental noise is presented in Tab: 3.1

to increase the variance in comparison with the effect of adding white and pink noise (see Table 3.2).

- The Ricker model shows strong persistence in all the realizations during the 20 years of the simulation time interval. The logistic model shows very week persistence in comparison with Gompertz model in all the realizations during the 20 years of the simulation time interval.

3.5 Extinction probabilities

Volker and Christian analyse the mean time to extinction by considering in their analysis only the populations for which actual extinction happened, and ignoring the persisting populations [84]. Here we analyse the distribution of extinction and persistence probabilities using the same method as [84], but including the persisting population. The study is given in the following steps,

1. Write a program to simulate the population dynamics for a long period of time, say 300 years.

2. Repeat the program at least 1000 times and record the time when each population goes extinct, without ignoring when the populations that persist for 1000 years; i.e. when and/or whether each population goes extinct.

3. Generate a histogram of extinction times, and normalize the histogram by dividing all histogram bars by the total number of simulation runs.

4. Estimate the probability $p(t')$ of the population going extinct in the time interval t' from the normalized histogram bars. From this, we obtain the cumulative probability $P_0(t)$ of the population being extinct by time t' (i.e. the bars are successively added up to time t'). The final value in the cumulative probability plot is the total probability of extinction in 300 years.

$$C_D = P(E_h \leq t | E_h \leq T)P(E_h \leq T), \tag{3.8}$$

where C_D is the cumulative distribution function, and E_h represents when the extinction happens. Simply it means the probability if being extinct at time t, where $t \in [0, T]$.

Example 3.5.1. *Suppose we run* 1000 *simulations of the population dynamics for* 1000 *years. If* 150 *populations do not go extinct (persist for* 1000 *years), then* 850 *model populations must go extinct.*

Normalising the sorted data of yearly extinction event counts (dividing it by 1000*), and successively summing up the normalized probability will yield the total probability of going extinct in the next* 1000 *years:* 85%, *yielding a total persistence probability of* 1 − *total probability of extinction* = 15%.

A quasi-extinction level (QEL) is a threshold population size, chosen such that once the population reaches or falls below the QEL, extinction becomes highly likely, if not inevitably. The quasi-extinction level (QEL) helps to build a practical perspective of population viability analyses (PVA) in order to preserve endangered species.

In this section we estimate extinction and quasi-extinction probabilities for each of the models (quasi-extinction level of 5), including different colors of environmental noise (white, pink and red) in different positions. We perform similar simulations to those described above, but with quasi extinction we consider a population to be "extinct" when its size dips below the level 5.

Figure 3.8 shows cumulative extinction probabilities over 1000 years for the three models (logistic, Gompertz and Ricker), with demographic stochasticity, based on 1000 simulations per model.
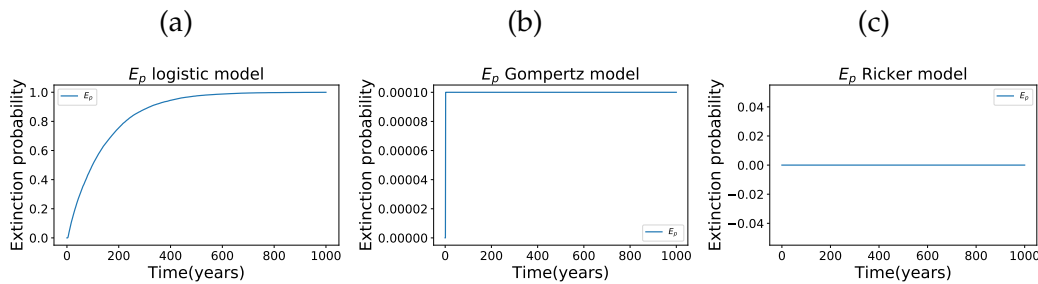
Figure 3.8 – Cumulative extinction probabilities of the logistic, Ricker and Gompertz models with demographic stochasticity. $N_0 = 10$, $k = 100$ and individual fitnesses are sampled from a Poisson distribution with $\lambda = 1.2$.

We used the cumulative distribution to find total extinction and persistence probabilities E_p and $P_p = (1 - E_p)$ for all the models. The extinction probability of each model is listed in Table 3.3. We notice that in the Gompertz

model, extinction happens only in the first few years of the simulations, since small population size increase the demographic stochasticity.
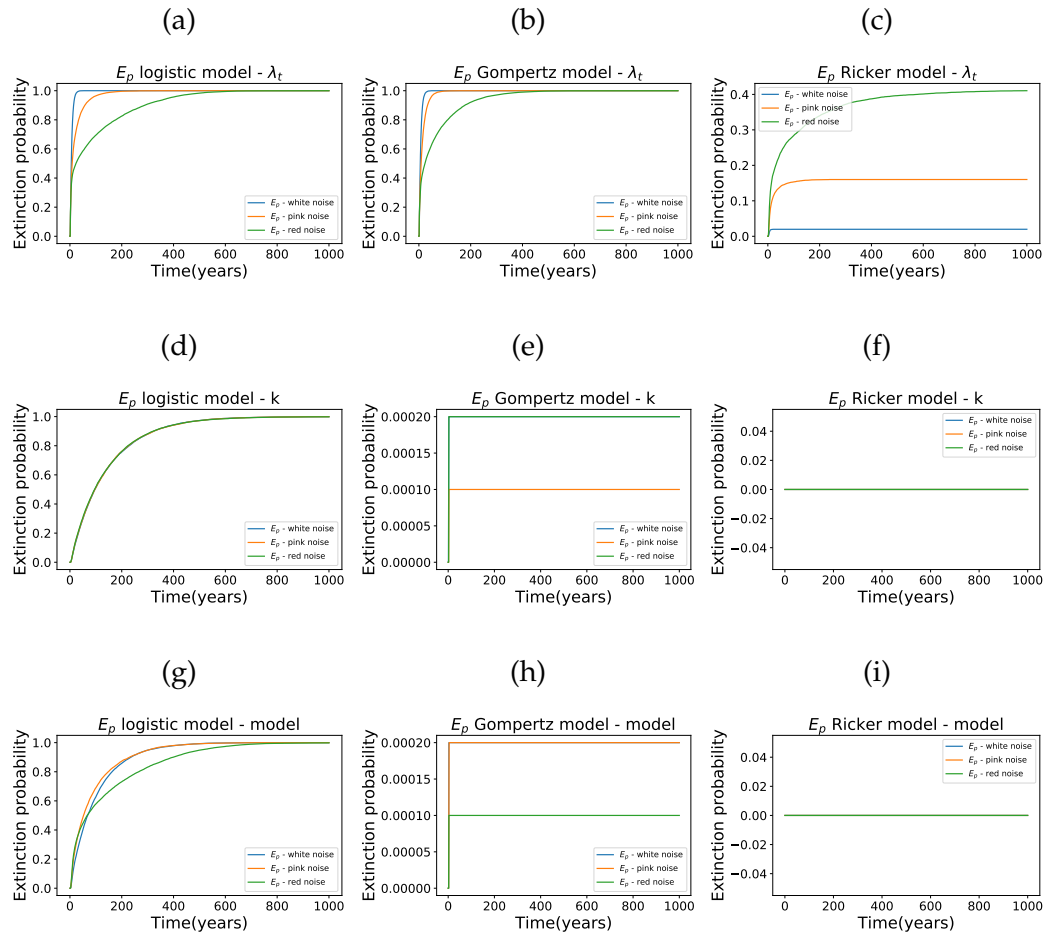
Figure 3.9 – Cumulative extinction probabilities as functions of time for logistic, Ricker and Gompertz models with red, pink and white environmental noise in different positions, and demographic growth rate. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$, and mean individual fitness $\lambda = 1.2$. Each point represents the average of 1000 simulations, run for 1000 years.

Figure 3.9 below shows cumulative extinction probabilities for the three models, with white, pink and red environmental noise. We again used the cumulative distribution to find the extinction probability E_p and the persis-

tence probability $P_p(1 - E_p)$ for all the models. Extinction probabilities are listed in Table 3.3.

From the extinction probability Figure 3.9: Ricker model has the highest persistence rate among the three models followed by Gompertz and lastly logistic model. Surprisingly, regardless of the colour of the environmental noise, Ricker and with the noise added to the model or to *k* has the same extinction probability. Red environmental noise results in a lower extinction rate in comparison with white and pink noise in all the models.
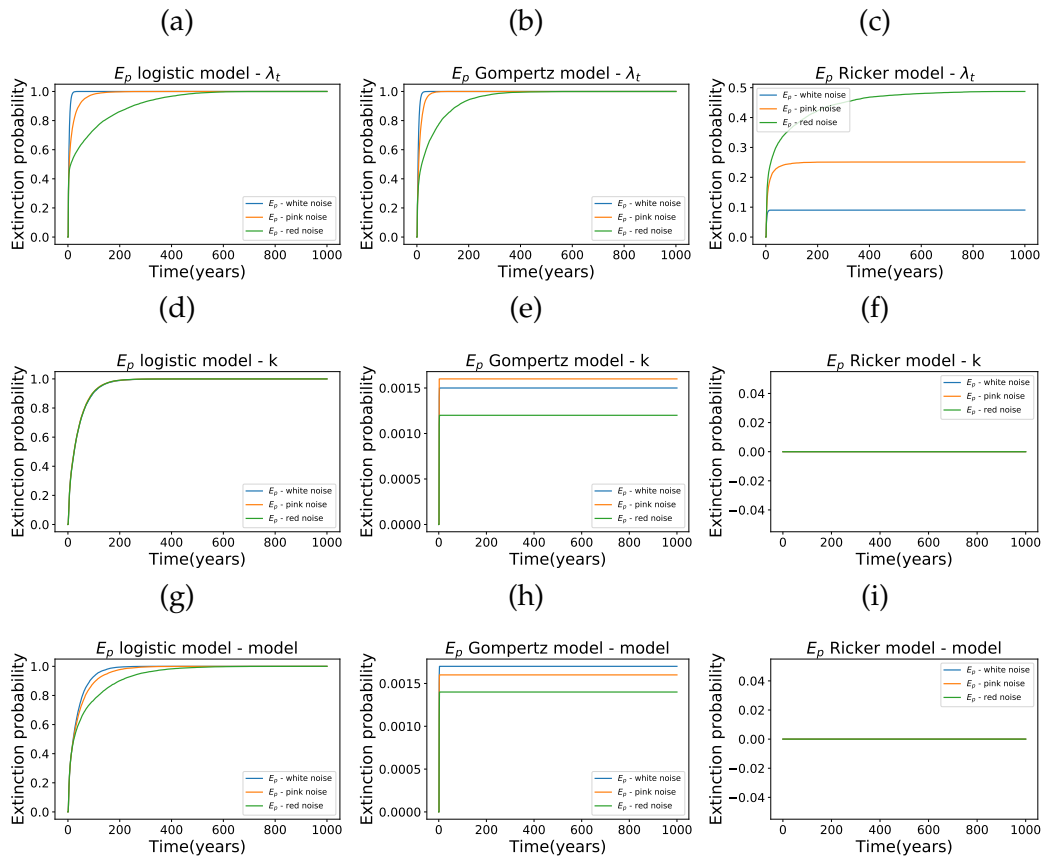
Figure 3.10 – Cumulative quasi-extinction probabilities as functions of time for logistic, Ricker and Gompertz models with red, pink and white environmental noise in different positions. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$ and base carrying capacity $k = 100$. Each curve represents the average of 1000 simulations, run for 1000 years.

Model \ Noise	Demographic stochasticity	White		Pink		Red	
		λ_t	Model	k	λ_t	Model	k	λ_t	Model	k

Model \ Noise	Demographic stochasticity	White λ_t	White Model	White k	Pink λ_t	Pink Model	Pink k	Red λ_t	Red Model	Red k
Logistic	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
Gompertz	0.01%	100%	100%	100%	100%	0.02%	0.01%	100%	0.01%	0.02%
Ricker	0%	41%	16%	2%	0%	0%	0%	0%	0%	0%

Table 3.3 – Numerical calculation of extinction probabilities for demographic stochasticity (second column in the table); demographic stochasticity and three different environmental noises in different positions (column 3 to 5 in the table).

3.6 Sensitivity to demographic stochasticity and environmental noise

3.6.1 Demographic stochasticity

In this section, we use the logistic, Gompertz and Ricker models with yearly fluctuations in the demographic rate caused by demographic stochasticity affecting the growth. We simulate the distribution of the extinction probability and the mean and variance of the population sizes on a 1000 simulations per parameter value, each for 300 years.
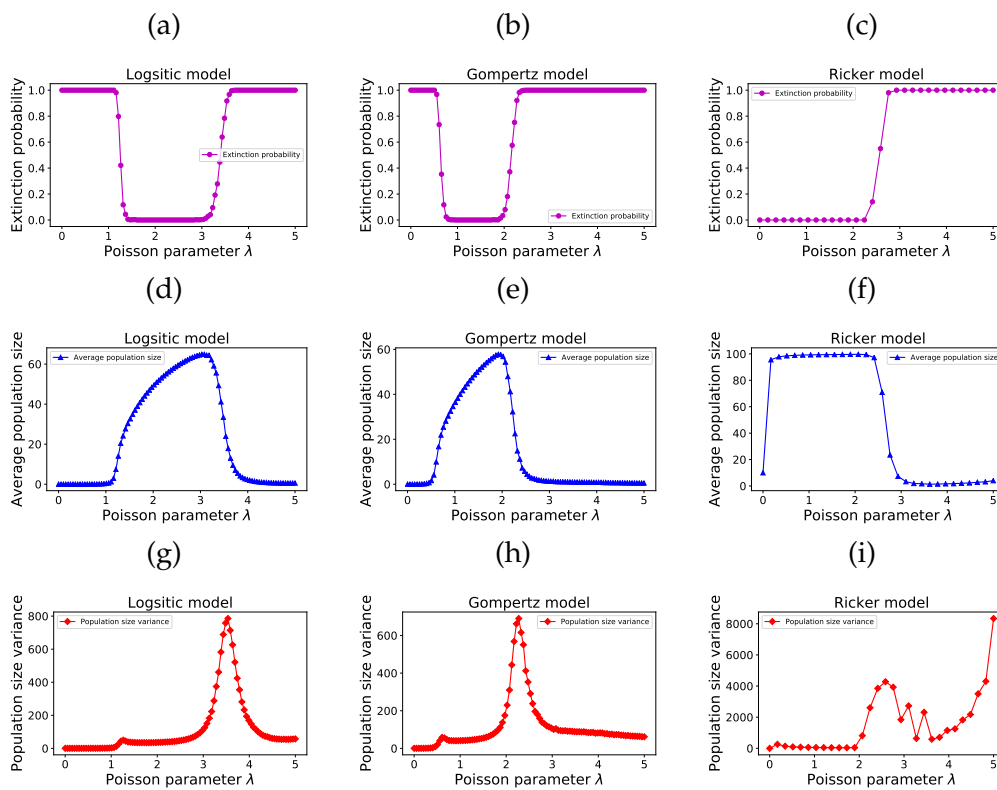
Figure 3.11 – Extinction probability, average population size and population size variance as functions of the mean individual fitness λ_t. In the logistic and Gompertz models, population variances increase with λ_t up to critical values, which correspond to the critical λ_t values for extinction. Interestingly, the Ricker model does not exhibit this despite similar behaviour in terms of extinction probability and average population size.

The initial population size is 10, and the carrying capacity is 100. The demographic growth is extracted from Poisson distribution with $\lambda \in [0, 5]$. We

only applied a demographic stochasticity to the three models.

The exponential nature of the Ricker model ensures much higher persistence up to a critical value of approximately 2.6, after which the population goes extinct due to the crowding effect. In the logistic and Gompertz models, the range of the persistence window is smaller than that in the Ricker model. In the logistic and Gompertz models, the average population size and variance increases with λ up to critical values, which correspond to the critical λ values for extinction. Interestingly, the Ricker model does not exhibit this despite similar behaviour in terms of extinction probability and average population size.

3.6.2 Demographic stochasticity and white environmental noise

To explore the effects of adding noise to the logistic, Gompertz and Ricker models, we simulated the population dynamics for 300 years with demographic and white environmental noise. We varied the variance of the environmental noise, and added the noise to different positions in the models. When adding the noise to the growth rate λ_t we explored variances $\sigma^2 \in [0, 6]$; when adding the noise to the model or into k we explored variances $\sigma^2 \in [0, 30]$. We calculated the extinction probabilities, average population sizes[1] and total population variances based on a 1000 simulations for 300 years of reproduction.

For all simulations, we used an initial population size $N_0 = 10$ and a base carrying capacity $k = 100$. The demographic growth is extracted from a Poisson distribution with $\lambda = 1.2$. White noise is generated from a normal distribution with zero mean and constant variance.

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[1]Average population sizes include populations which go extinct, so average population size is a combination of extinction probability, time to extinction and the sizes of populations which survive.
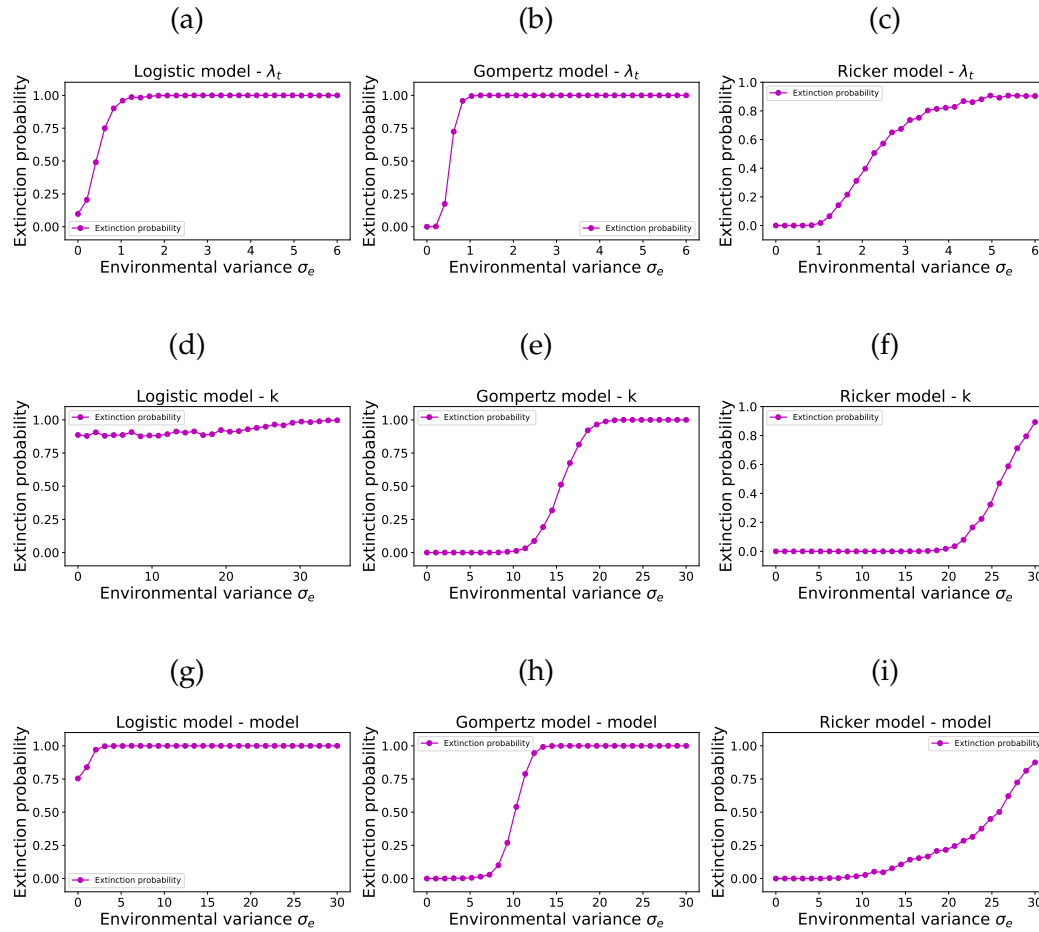
Figure 3.12 – Total extinction probability over 300 years of logistic, Ricker and Gompertz models with demographic and white environmental noise, as functions of the variance of the environmental noise. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$, and mean individual fitness $\lambda = 1.2$. Each curve represents the average of 1000 simulations.

Increasing the variance of environmental noise increases the extinction risk in all the models and in all the noise positions (λ_t, k and directly to the model). Including white noise in the demographic growth λ_t for the logistic and Gompertz models results in a smaller variance interval $\approx [0, 1.2]$ for which population persistence is possible, while it is $\approx [0, 6]$ in Ricker model. In other words, it appears the Ricker model is appropriate for modelling populations which can tolerate high population variance driven by

environmental noise. The risk of extinction when adding noise to λ_t is very high compared to the risk when adding noise into the carrying capacity k or directly to the model. The average of population size decreases with increasing noise variance in all the models. This is unsurprising, since as the level of environmental variance increases, the likelihood of extreme events will also increase.
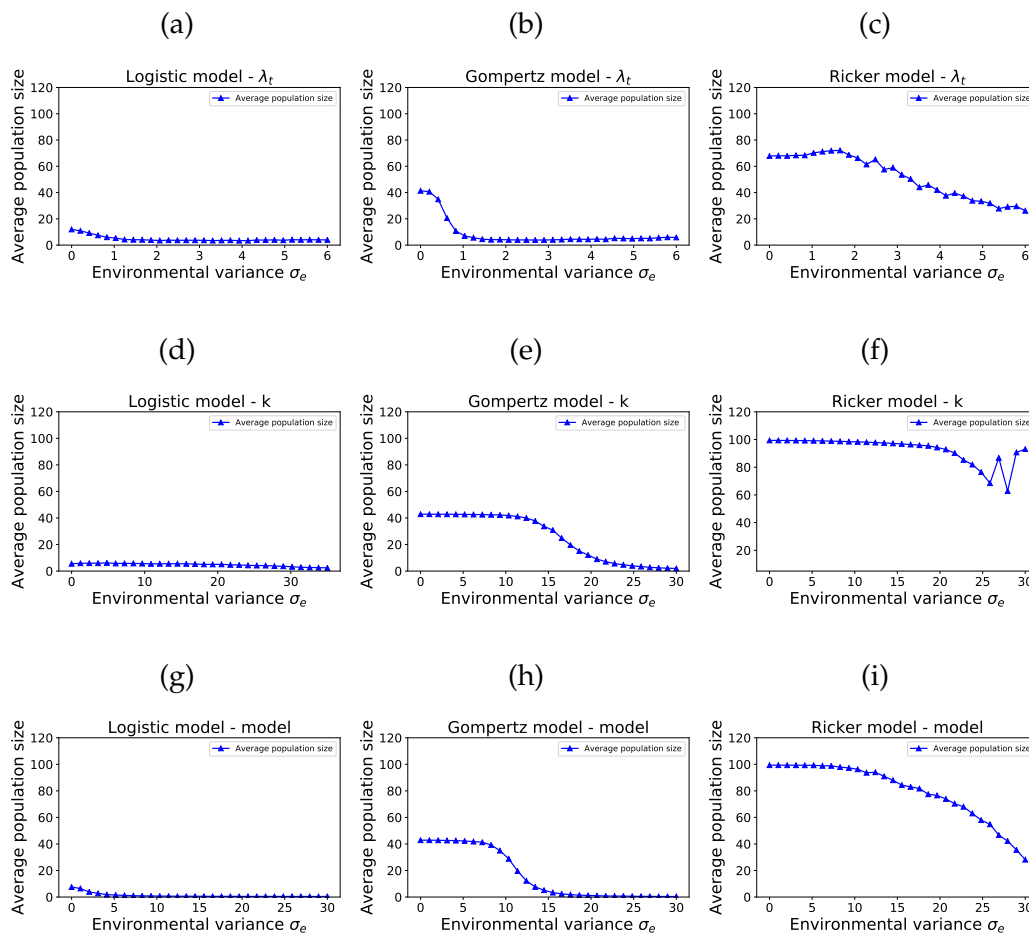
Figure 3.13 – Average population sizes for $300-$year; 1000 simulations of logistic, Ricker and Gompertz models with demographic and white environmental noise, as functions of the variance of the environmental noise. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$, and mean individual fitness $\lambda = 1.2$.
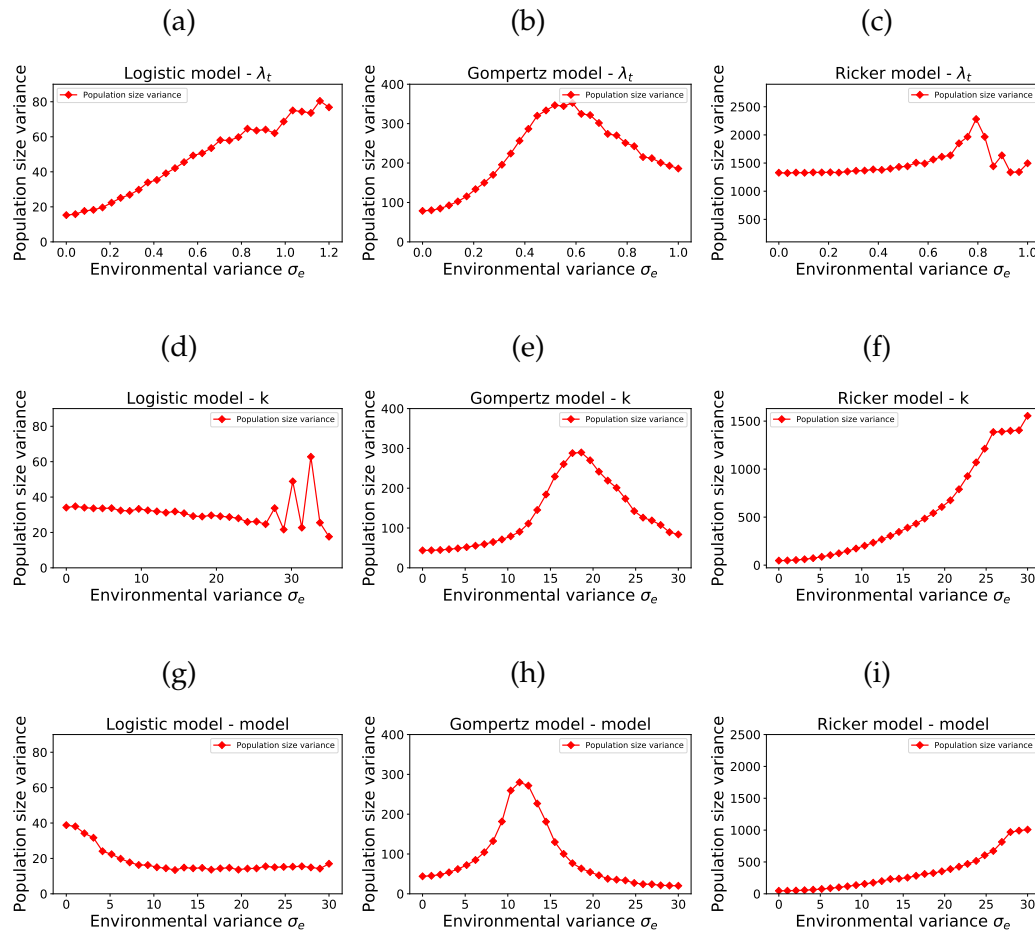
Figure 3.14 – Population size variances of logistic, Ricker and Gompertz models with demographic and white environmental noise, as functions of the variance of the environmental noise. In the first row the environmental noise is added to the growth rate λ_t; in the second row it is added to the model; in the third row it is added to the carrying capacity. In all cases initial population $N_0 = 10$, base carrying capacity $k = 100$, and mean individual fitness $\lambda = 1.2$. Each point represents the average of 1000 simulations of 300 years.

3.6.3   Demographic stochasticity and coloured environmental noise

In this section, we simulate the dynamics of the logistic, Ricker and Gompertz models with demographic stochasticity and coloured environmental noise, exploring values of the power-law exponent $\beta \in [-1, 5]$ (e.g. $\beta = 0$ gives white noise, $\beta = 1$ pink noise and $\beta = 2$ red noise). We observe

the distributions of extinction probability and, average population size and total population variance based on 1000 simulations per β value, each run for 300 years. In all cases the initial population size $N_0 = 10$ and carrying capacity $k = 100$. The individual fitness values are sampled from a Poisson distribution with mean $\lambda = 1.2$. The autocorrelation observed in the coloured noise time series varies in the interval $[-0.8, 0.95]$.
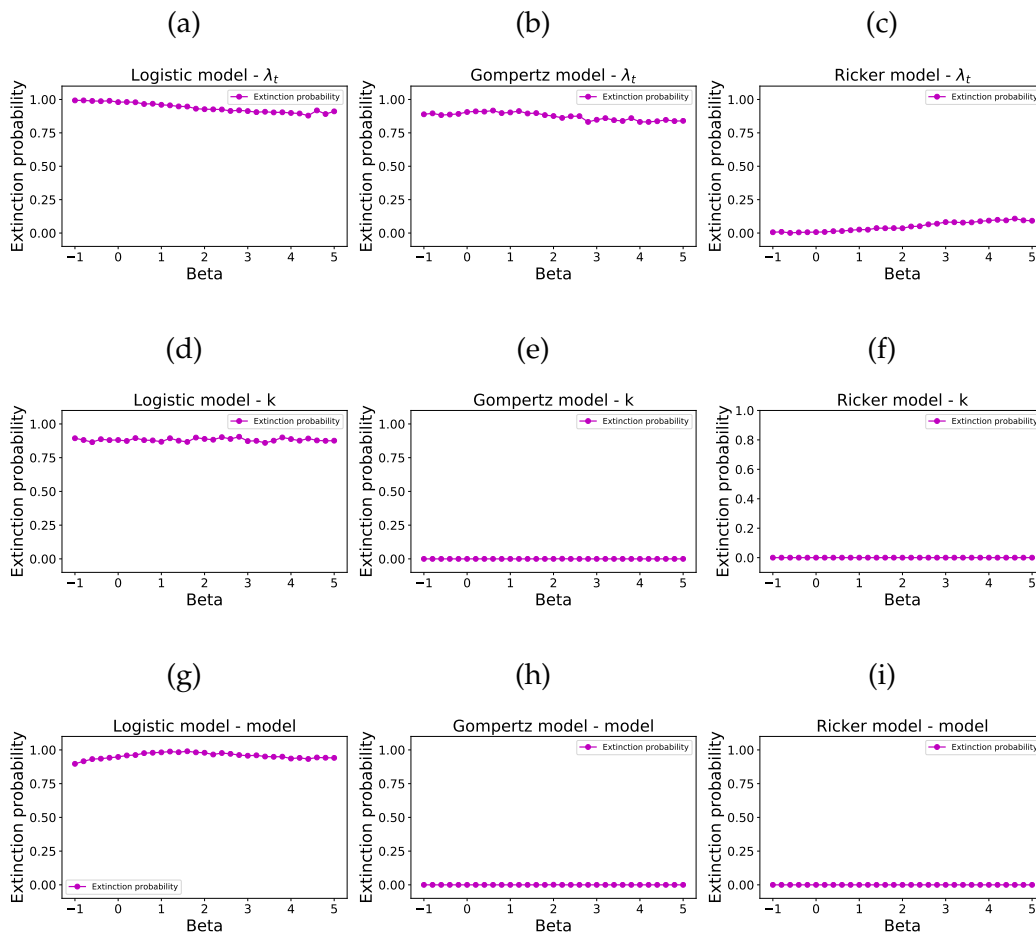
Figure 3.15 – Extinction probability of Logistic, Ricker and Gompertz model with demographic and environmental noise, the power low of the noise frequency β of the environmental noise in range $[-1, 5]$. The first column, the noise added to the model; the second column, the noise added to the model and in the third column, the noise is added to the carrying capacity. The initial population size is $N_0 = 10$ and the carrying capacity is $k = 100$ for period of 300 year. The plots shows the last year prediction.
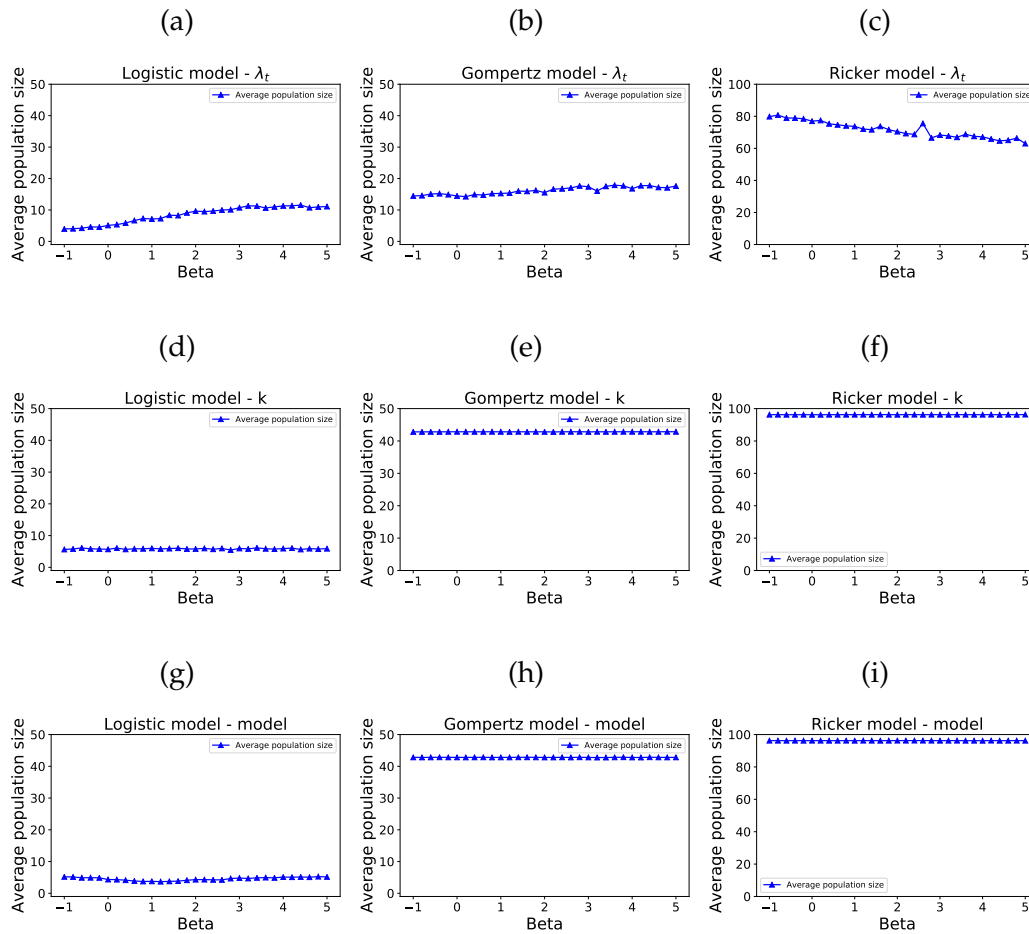
Figure 3.16 – The population size variance in Logistic, Ricker and Gompertz model with demographic and white noise environmental noise. the power low of the noise frequency β of the environmental noise in range $[-1, 5]$. The first column, the noise added to the model; the second column, the noise added to the model and in the third column, the noise is added to the carrying capacity. The initial population size is $N_0 = 10$ and the carrying capacity is $k = 100$ for period of 300 year. The plots shows the last year prediction.

The Gompertz and Ricker models show increasing population persistence with increasing β-values when the noise is added to k or directly to the model. In all three models, when adding the noise into the demographic growth rate λ_t, increasing β increases the risk of extinction as well as the population variance and, in the logistic and Gompertz models, the average population size. This could suggest that a higher proportion of extinctions may be driven by overpopulation rather than low reproductive rates, when

β-values are high. In the Ricker model however, the average population size is decreases with increasing β, though the total population variance is increased with increasing β. The Ricker and Gompertz model exhibit high persistence compared with the logistic model throughout the range of β values.
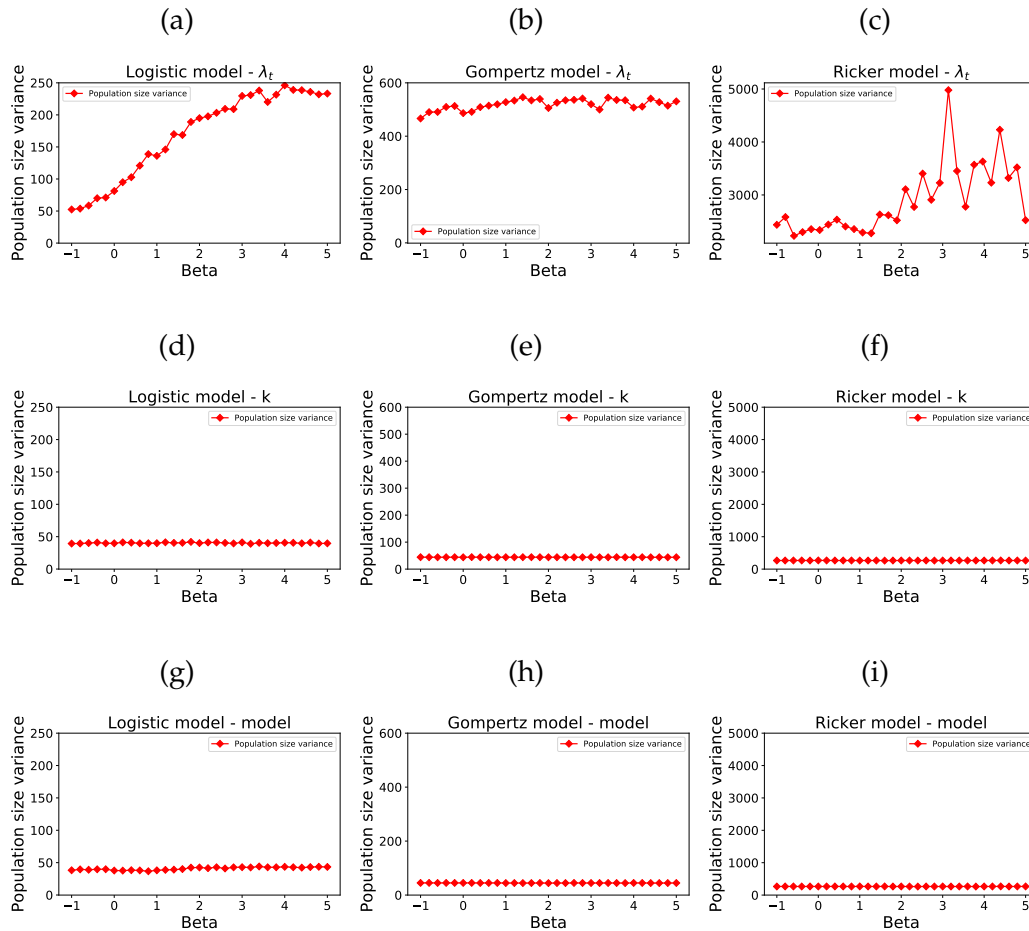
Figure 3.17 – The population size variance in Logistic, Ricker and Gompertz model with demographic and white noise environmental noise. the power low of the noise frequency β of the environmental noise in range $[-1, 5]$. The first column, the noise added to the model; the second column, the noise added to the model and in the third column, the noise is added to the carrying capacity. The initial population size is $N_0 = 10$ and the carrying capacity is $k = 100$ for period of 300 year. The plots shows the last year prediction.

3.7 Population viability analysis

Population viability analysis (PVA) is based on biological and mathematical principles which are used together in assessing the extinction risk for a population of interest. It is a test to characterise the factors that are most important for the population's survival. Generally speaking, there are two principal factors which influence the population viability: the demographic rates and the temporal environmental variability [5, 21]. The temporal environmental variability is always accounted for when conducting a PVA, independent of the population size or structure, while demographic rates are considered particularly important when population size is small. Small populations are naturally vulnerable (i.e. closer in number to extinction), and in addition face larger demographic stochasticity; they are also subject to environmental stochasticity, though in some cases this may be reduced in smaller populations. The main factors influencing the distribution of extinction risk:

1. The stochastic growth rate λ_t and its variance are two important factors in determining the distribution of extinction probabilities.

2. Stochastic variations in the growth rate may be due to:

   - Density-independent factors such as the variation in the environmental conditions from year to year, or catastrophes (i.e. extreme events).

   - Density-dependent factors and effects such as resource shortages, predation, parasitism, and demographic stochasticity (chance variation in births and deaths).

3. The life history and current population size.

3.7.1 The use of PVA

PVAs may be used to:

1. Estimate the probability distribution of future population sizes (implicitly including extinction risk).

2. Compare the relative risk between populations in the community. We can attempt to predict whether or not there will be a decline in all

or most of the populations in a given habitat. Furthermore, we can estimate our probability of success if we attempt to save particular (or all) populations in the habitat, and which populations need to receive the management attention first. We can also select most promising populations after determining which population we could save and which we could not.

3. Determine the relative risk of the community members, for example, we can estimate the probability distribution of the community members, i.e., whether the community persists or not.

4. Determine how many years of the censused data would be required to make reasonable conclusions about the population growth, survival, and reproduction and inform habitat conservation plans and management decisions.

5. Determine and identify the contributions from each life stage to the population growth, and inform targeted management or intervention.

6. Estimate the optimal number of individuals to release in order to establish a new population, or the number of individuals that may be removed from existing population without endangering the remaining population.

7. Determine how large a reserve is needed to gain a desired level of protection from extinction. If we can estimate the amount of space each individual needs, we may use PVA models to ask how large the area of the reserve should be (or of what quality, given a fixed size) to achieve low probability of extinction risk for certain population.

8. Set limits on the allowed harvest from a population that are compatible with its continued existence. Direct harvesting reduces the population size and thus increases the extinction risk. The same applies to other causes of indirect mortality related to human activity.

9. Decide how many populations are needed to protect a species from regional or global extinction. We can combine the analyses of extinction risk for populations, and identify the probability that at least one population will continue to exist at a given future time. We might ask how

much safety from extinction an entire species could gain if we were to preserve particular numbers and combinations of extant populations.

3.7.2 Assumptions in PVAs

PVAs may be conducted under various sets of assumptions, and there is to this day no generalized rule or clear set of common assumptions for PVAs. Choices of assumptions depend on the dynamics of the particular populations under consideration, as well as the availability of environmental and demographic data [57]. Nonetheless, we cite some common assumptions used in previous PVAs:

3.7.2.1 Common assumptions of PVAs utilising density-independent models

1. The parameters μ and σ^2 are constant over time, and independent of the population size.

2. The population growth rate is independent of the population size i.e. there is no density dependence.

3. The demographic stochasticity is ignored for the derivation of extinction probability formula. Environmental trends are ignored.

3.7.2.2 Common assumptions of PVAs utilising density-dependent models

1. The parameters μ and σ^2 are constant over time.

2. There is no autocorrelation in the environmental noise; in most analyses only white noise is considered.

3. There are no extreme events (catastrophes) or bonanzas (good years). Catastrophes, such as ice storms, wildfires, droughts cause rapid reduction in population sizes, while bonanzas such as (good years) may cause high levels of reproductive success/survival. In these analysis, the extinction probability is derived under the assumption of only small changes to the base parameter values, causing relatively low rates of change in the population size.

4. No observation error: observed population sizes are treated as true
   population sizes.

5. All individuals are modelled as identical, and populations are without
   structure.

3.7.3 Minimum viable population size (MVP)

A minimum viable population is a threshold number of individuals suffi-
cient to maintain a population. It is a crucial level for which the extinc-
tion probability is sufficiently small and should ensure a high survival rate
over a specified time interval.The existence of a minimum viable population
(MVP), implies that there is some threshold population size which ensure a
high survival probability of the population for some given time interval, de-
spite the effects of demographic and environmental noise as well as natural
catastrophes [70].

3.8 The theory of the mean time to extinction

The mean time to extinction in population growth models depends mainly
on the carrying capacity K and the mean growth rate λ. In deterministic
models, the growth rate is the key feature of determining whether the pop-
ulation will go extinct: if $(\bar{\lambda} < 1)$, i.e. the population has an average growth
rate of less than one, the population will go to extinction in a time period
proportional to the logarithm of the initial population size N_0. If $\bar{\lambda} > 1$
the population will continue growing to an infinite time when we use the
simple exponential model $(\frac{dN}{dt} = \bar{\lambda}N)$, or stay at the carrying capacity for-
ever when we use the logistic, Ricker, Gompertz (or almost any density-
dependent) model.
Russel Lande [42] manages to estimate the mean time to extinction for the
ceiling model; he concludes that the mean time to extinction is either expo-
nential of carrying capacity or is a power of (k^c). He spotted that the differ-
ences in the mean time to extinction distribution can be understood based
on the mean and the variance of the long-term population growth rate λ.

By using the diffusion approximation and with the condition $\bar{\lambda} \geq \sigma^2$, the
mean time to extinction MTE shows a convex relationship with the carry-

ing capacity K. Otherwise, MTE curves have a concave relationship with K, unless there is a high correlation in the environmental noise [42]. The variation in environmental noises and the growth rates explain why carrying capacity and mean time to extinction have different relationships when we assessing the population viability analysis.

Ovaskainen & Meerso [67] deduce two different assumptions to analyse the mean time to extinction (MTE), and that variation is according to the model description, whether environmental noise is present or not.

1. Under the first assumption, i.e., if there is no environmental noise, then the mean time to extinction (MET) is proportion to the exponent of K, [67], and is represented by,

$$\begin{cases} MTE = C_1(\lambda_t, K)e^{b(\lambda_t, v_d)K}, \\ b(\lambda_t, v_d) = \frac{\bar{\lambda}}{\sigma_d^2}, \end{cases} \tag{3.9}$$

   Equation (3.9) shows that the constant C_1 is depends on the carrying capacity and the growth rate λ_t. b is depend on the growth rate λ_t, and the variance of the demographic noise σ_d^2.

2. With uncorrelated environmental noise, MET is proportional to K^c [67], and it is given by,

$$\begin{cases} MTE = C_2(\lambda_t, K)K^{C(\lambda_t, v_e)}, \\ c(\lambda_t, v_d) = \frac{2\bar{\lambda}}{\sigma_e^2}, \end{cases} \tag{3.10}$$

Equation (3.10) shows that the constant C_2 is same as C_1 depends on the carrying capacity K and the growth rate λ_t. The constant c is depend on the growth rate λ_t, and the environmental noise variance σ_e^2.

(a)

(b)
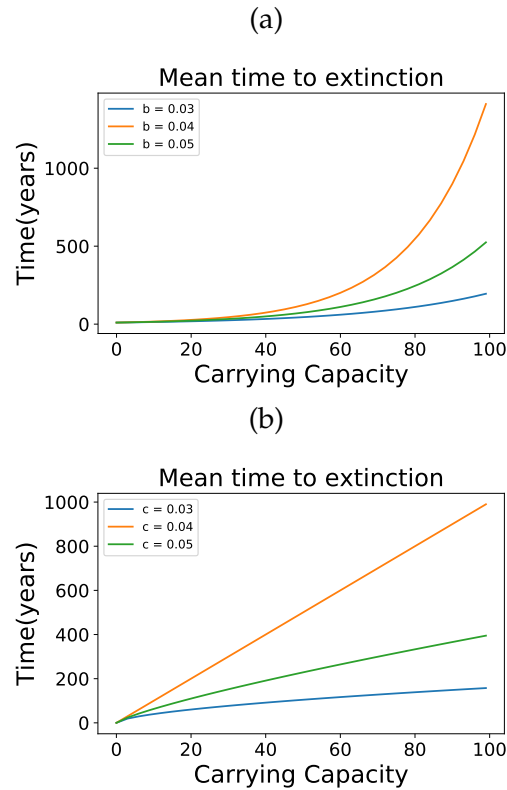
Figure 3.18 – Simple illustration of the MTE, the parameter b have the values $[0.03, 0.04, 0.05]$, the parameter c has the values $[0.3, 0.4, 0.5]$, $C1 = C2 = 10$. Note that b and a are depends on the growth rate and the variance of the environmental and demographic noise.

3.9   Results

To explore the problem of assessing extinction risk with demographic and environmental variability, we compared mean extinction times in white, pink and red noise environments. We find large differences in the probabilities of extinction and persistence between the three models, and observe that:

1. The logistic model exhibits the slowest average growth rate.

2. The Ricker model has the highest persistence, followed by Gompertz model.

3. The logistic model exhibits different behaviour with white, pink and red environmental noise. Populations tend to persist in environments

with coloured noise.

4. Coloured noise promotes extinction in the Ricker model when added to λ_t.

The common results from the simulations are as follows.

1. If the growth rate λ_t is negative, eventually the population goes extinct, independent of the variance of the growth rate.

2. If the growth rate λ_t is positive, there is still a risk of falling the under the quasi-extinction level where there is no recovery.

3. Extinction risk depends on the average growth rate, and the variance of the growth rate.

4. In small populations, the demographic noise reduces the population growth rate, therefore increases the extinction risk.

5. The variance of environmental fluctuations is an important feature in determining extinction risk; high variance directly increases the extinction risk of a population (figure 3.12).

6. High levels of autocorrelation in coloured environmental noise appear to promote population persistence, even though sometimes the correlation of bad years causes extinctions which might not have otherwise occurred.

Chapter 4

Stochasticity in Competition Models

4.1 Outline

In this chapter, we study the effects of demographic and environmental stochasticity in the logistic, Gompertz, and Ricker competition models. The rest of the chapter is laid out as follows. We begin with some theoretical background on which to build our stochastic competition models. We then run simulations with the three models, exploring the effects of demographic stochasticity alone. We also run simulations with correlated and uncorrelated white environmental noise. We explore the effects of these forms of noise on the probability distributions of extinction risk, average population size and total population variance.

4.2 Model descriptions

In this section, we give a short description of the logistic, Gompertz, and Ricker models with two competing species. We describe the incorporation of various types of stochasticity in these models.

4.2.1 Logistic Lotka-Volterra model

In real life, many species compete for limited resources - primarily food, water and nesting space. Lotka Volterra competition models are widely used to model systems of two or more interacting populations, such as populations

47

competing for access to resources (or otherwise inhibiting one another). The Lotka Volterra equations were independently derived by Alfred Lotka and by Vito Volterra in 1925 and 1926 respectively, and are some of the most famous equations for modeling ecological dynamics [16, 17, 40]. We utilise a stochastic logistic Lotka-Volterra competition model of the form:

$$N_{i_{t+1}} = \lambda_{i_t} N_{i_t} (1 - (\frac{\sum_{j=1}^{n} \alpha_{i,j} N_{j_t}}{k_i})), \tag{4.1}$$

Our goal here is to investigate the dynamics of two competing species experiencing demographic stochasticity and environmental noise.

Suppose we have two competing populations, where N_1 and N_2 represent the population sizes. The Lotka-Volterra model for this situation would include two interspecific interaction terms, in addition to the intraspecific interaction terms of the single-population logistic model. We use a two-species competitive Lotka-Volterra model of the form:

$$N_{1_{t+1}} = \lambda_{1_t} N_{1_t} (1 - \frac{\alpha_{1,1} N_{1_t} + \alpha_{1,2} N_{2_t}}{k_1}) \tag{4.2}$$

$$N_{2_{t+1}} = \lambda_{2_t} N_{2_t} (1 - \frac{\alpha_{2,1} N_{1_t} + \alpha_{2,2} N_{2_t}}{k_2}), \tag{4.3}$$

where the inter-specific interaction coefficients $\alpha_{i,j} > 0$ represent the effect of species j on species i. The coefficient $\alpha_{i,i}$ represents the effect of species i on itself (intraspecific), and we set $\alpha_{i,i} = 1$ in all cases. The α-values do not have to be equal. We set $\alpha_{i,j} > 0 \ \forall i, j$ since the interspecific interaction is competitive, and each population will inhibit the other's growth. We refer to the population exerting the larger competitive pressure as the 'stronger' population and the population experiencing the larger competitive pressure as the 'weaker' population. The competition interaction coefficients are assumed to be fixed over the course of each simulation. In our simulations, each species has its own growth rate λ_t, but the same carrying capacity ($k_1 = k_2$).

The deterministic model suggests four expected outcome for competition models, $\alpha_{1,2}, \alpha_{2,1} < 1$ the two population would be able to coexist together. $\alpha_{1,2}, \alpha_{2,1} > 1$ both population are endangered. In case of $\alpha_{1,2} > 1$ and $\alpha_{2,1} < 1$, population 2 would be dominant and effect the other population negatively, causing extinction of population 1.

4.2.2 Ricker competition model

The general form of the discrete stochastic Ricker competition model has for each population an equation of the form:

$$N_{i_{t+1}} = N_{i_t} e^{\lambda_{i_t}(1-(\frac{\sum_{j=1}^{n} \alpha_{i,j} N_{j_t}}{k_i}))}. \tag{4.4}$$

We investigate the dynamics of the Ricker model having two competing populations with various types of environmental and demographic stochasticity. N_1 and N_2 represent the abundance of population one and population two, respectively. The Ricker model for two competing species is given by:

$$N_{1_{t+1}} = N_{1_t} e^{\lambda_{1_t}(1-\frac{N_{1_t}+\alpha_{1,2} N_{2_t}}{k_1})} \tag{4.5}$$

$$N_{1_{t+1}} = N_{2_t} e^{\lambda_{2_t}(1-\frac{\alpha_{2,1} N_{1_t}+N_{2_t}}{k_2})}, \tag{4.6}$$

where $\alpha_{i,j} > 0$ represents the competitive impact of population j on population i.

4.2.3 Gompertz competition model

The general form of the discrete stochastic Gompertz competition model has for each population an equation of the form:

$$N_{i_{t+1}} = \lambda_{i_t} N_{i_t} (\log(\frac{k_i}{\sum_{j=1}^{n} \alpha_{i,j} N_{j_t}})), \tag{4.7}$$

We investigate the dynamics of the Gompertz model with two competing population with various types of environmental and demographic stochasticity. N_1 and N_2 represent the abundance of population one and population two, respectively. The Gompertz model for two competing species is therefore given by:

$$N_{1_{t+1}} = \lambda_{1_t} N_{1_t} (\log(\frac{k_1}{N_{1_t} + \alpha_{1,2} N_{2_t}}), \tag{4.8}$$

$$N_{2_{t+1}} = \lambda_{2_t} N_{2_t} (\log(\frac{k_2}{\alpha_{2,1} N_{1_t} + N_{2_t}}), \tag{4.9}$$

where $\alpha_{i,j} > 0$ represents the competitive impact of population j on population i.

4.2.4 Correlation between environmental noise series

Correlation coefficients are used to measure the direct relationship between two time series: they describe how two time series are actually linked. Time series data are positively related if they move in the same direction (i.e increasing and decreasing at the same time) and are negatively (or inversely) related if they move in opposite directions (i.e. one increases when the other decreases).

Correlation between the effects of unpredictable environmental conditions occurs widely in nature: bad weather is often bad for a wide variety of populations, and good weather is often good for many in the community. The specific effects for each population will however vary, and will not necessarily be the same. The level of correlation between them may vary widely from situation to situation, but for species with similar life histories the correlation is likely to be large. In the following sections of environmental noise analysis, we explore the effects of correlated as well as uncorrelated white noise in the competition models.

4.3 Results and discussion

4.3.1 Demographic stochasticity

We simulate the three models with only demographic stochasticity for 100 years. We calculate the extinction probabilities, average population sizes and total population variances. The demographic growth is calculated based on individual fitness values sampled from a Poisson distribution with mean $\lambda \in [0,5]$.

The two species coexistence window for logistic and Gompertz models are $\approx (\lambda_1 \in [1.5, 3.1], \lambda_2 \in [1.2, 3.7])$ and $(\lambda_1 \in [1, 1.9], \lambda_2 \in [0.6, 2.2])$ respectively (Figures 4.1). Coexistence within these windows occurs only when λ_1 is slightly larger than λ_2, i.e. along a line with a slightly smaller slope than the dotted lines in Figure 4.1. The Ricker model exhibits starkly different behaviour: population 1 persistence range is depend on population 2 existence, and regions of coexistence are relatively small. The largest region of probable coexistence occurs when λ_1 is small (< 1) and $\lambda_2 \in [1.7, 2.7]$, but even here the compromise between survival of the two populations is evident. Population 1 persists for a very small range of λ_2, when λ_1 is small,

but persists for a much larger range of λ_2 ($[0, 1]$) when λ_1 is quite large (> 3). As might be expected, the overall area of parameter space for which the weaker population 1 persists is much smaller than that of population 2.
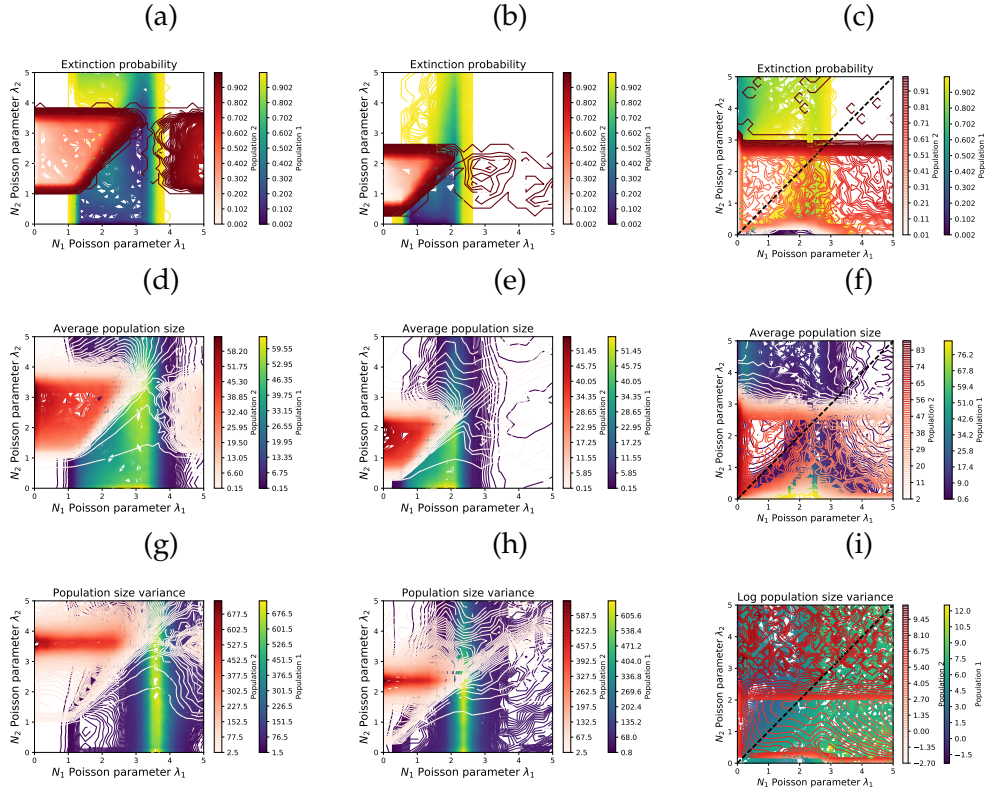
Figure 4.1 – Contour plots of extinction probabilities ($a - c$), average population sizes ($d - f$) and population variances ($g - i$) as functions of the mean demographic rate parameters λ_1 and λ_2 for models with demographic stochasticity only. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{2,1} = 1.5$ and $\alpha_{1,2} = 1.1$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

Also interesting is the strong boundary imposed on either population's survival by the other population's growth rate: when either population's growth rate is above three, the other population cannot persist. Since this effect does not depend on the persistence of the population with the large growth parameter, we hypothesize that these extinctions (of both populations) take place early in the simulations, driven by large fluctuations in the population(s) with the large growth parameter(s). The regions of applicability of the logistic and Gompertz models appear to be very similar - Figures 4.1a

and 4.1b are essentially scaled versions of one another, and quite separate from that of the Ricker model. The competition interaction is a core player in determining the fate of populations.

4.3.2 Quasi extinction probabilities

We simulate the three models with demographic stochasticity, uncorrelated white environmental noise and correlated white environmental noise.
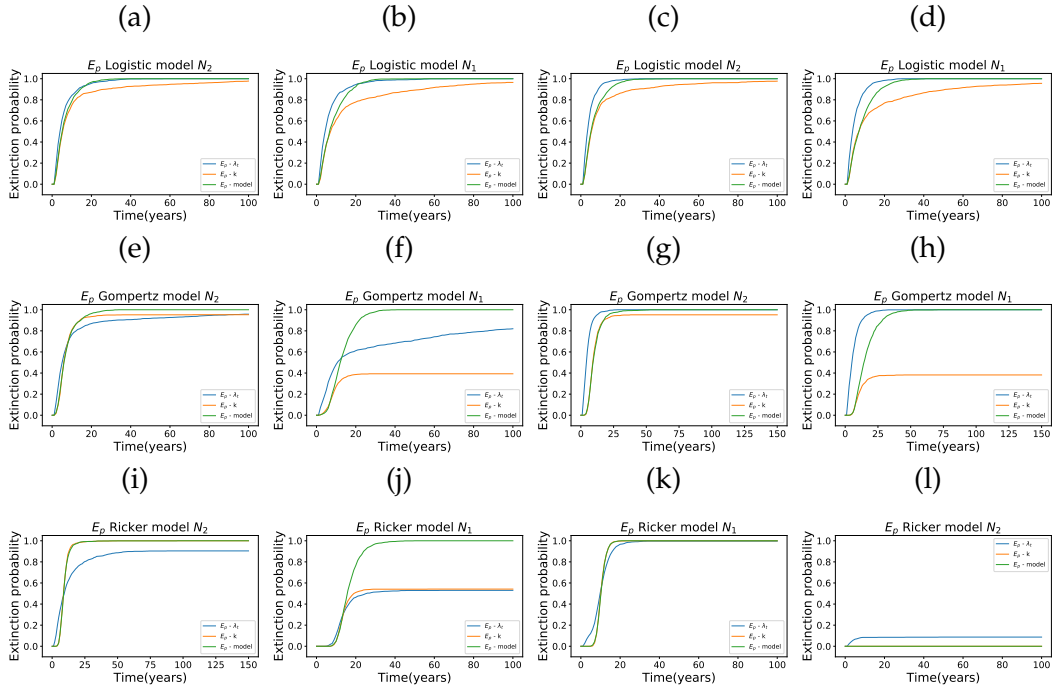
Figure 4.2 – Quasi-extinction probabilities of stochastic logistic, Gompertz and Ricker competition models with a quasi-extinction level of 5, including uncorrelated ($\rho = 0$, columns 1 & 2) and correlated ($\rho = 0.95$, columns 3 & 4) white environmental noise. Demographic stochasticity is sampled from Poisson distributions with $\lambda = 1.2$. We incorporated the noise in the growth rates λ_{1t} and λ_{2t}, in the carrying capacities k_1 and k_2 or added it directly to the models. Initial population sizes are $N_1 = N_2 = 10$, base carrying capacities are $k_1 = k_2 = 100$, and inter-specific interaction coefficients are ($\alpha_{1,2} = 1.1$, $\alpha_{2,1} = 1.5$). Results are the average of 1000 realizations, each run for 100 years.

We calculate the quasi-extinction probabilities of both populations, and compare between the simulations with correlated vs uncorrelated noise. In all the simulations, the initial population sizes $N_{1_0} = N_{2_0} = 10$, the carrying

capacity $k_1 = k_2 = 100$, and the environmental noise is generated from a normal distribution with zero mean and variance 0.4 for logistic and Gompertz models, variance 1 for Ricker model[1]. The demographic stochasticity is based on individual fitness values sampled from a Poisson distribution with mean $\lambda = 1.2$ for both population. We included the noise in the growth rates λ_{1_t} and λ_{2_t}, the carrying capacities k_1 and k_2 or added it directly to the models. Results are the average of 1000 realizations each run for 100 years, with a quasi-extinction level of 5. In all scenarios, we assumed population N_2 to be stronger, with $\alpha_{2,1} = 1.5$ and $\alpha_{1,2} = 1.1$.

The differences with these levels of environmental variances are relatively minor, but noticeable nonetheless. Perhaps most prominent is the increased relative extinction risk when noise is added to the growth rates, compared with the other positions (compare for example figure 4.2 *b* with *d*, *f* with *h*, or *i* with *k*). This makes sense: if both populations experience a boom at the same time, in the next time step each will experience an increased level of *both* intra-specific and inter-specific pressure. Adding noise to the growth rates caused the greatest volatility in Chapter 3, so it is to be expected that a small destabilizing factor will have more effect when involved in the growth rates than when added to the other positions. This idea is supported by the fact that the effect is least obvious for the logistic model, which exhibits generally slower and less volatile growth growth rate (see Chapter 2). Correlation in the Gompertz model has a much larger effect on population 2's persistence than on population 1's.

Once again we notice a stark qualitative difference between the Ricker and the other two models. In the Ricker model, environmental noise correlation causes *increased* risk for the weaker population 1, but *decreased* risk for population 2.

We repeat the procedure, this time looking only for "true" extinctions, i.e. with a quasi-extinction level of 1 (Figure 4.3). The results do not differ drastically from those calculated for a quasi-extinction level of 5.

In all three models the effects of the competition interaction terms are very clear, population 1 is driven very quick to extinction while population 2 persists for longer. The environmental noise has maximal effect when included in the growth rate λ_t.

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[1]We choose a variance values ($\sigma_e^2 = 0.4$ & 1) for which we could easily observe the differences between correlated and uncorrelated noise (see Figures 4.10, 4.11 & 4.12).
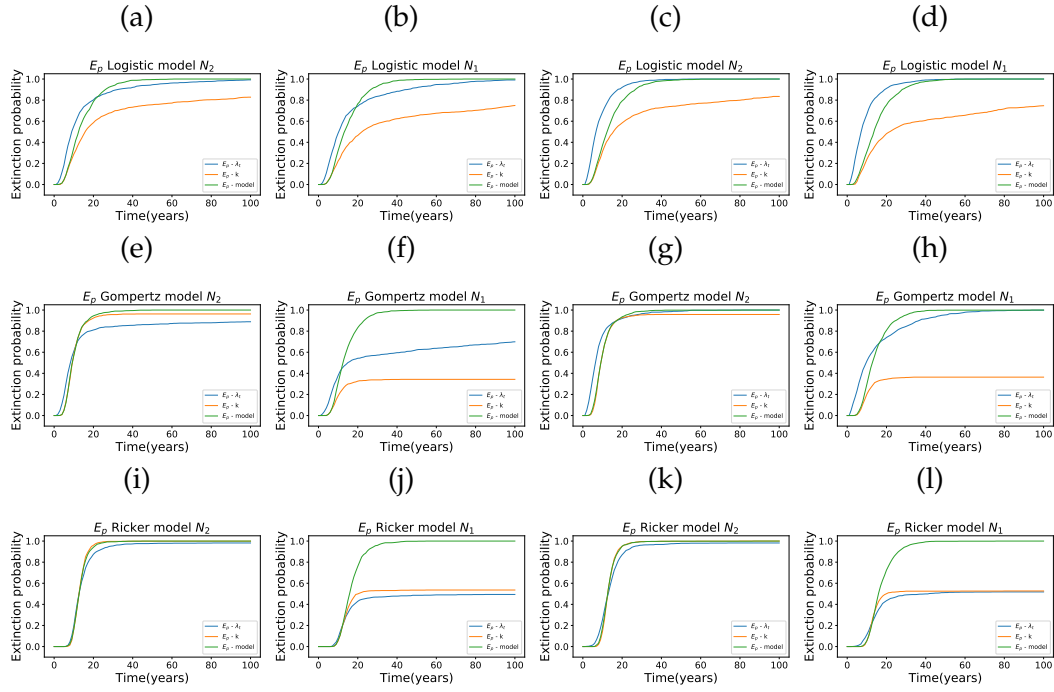
Figure 4.3 – Cumulative extinction probabilities of stochastic logistic, Ricker and Gompertz competition models with and uncorrelated ($\rho = 0$) and correlated ($\rho = 0.95$) white environmental noise. The individual fitnesses sampled from Poisson distributions with $\lambda = 1.2$. We added the noise to the growth rates λ_{2_t} and λ_{1_t}, directly to the models or to the carrying capacities k_1 and k_2. Initial population sizes are $N_1 = N_2 = 10$, base carrying capacities are $k_1 = k_2 = 100$, and inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$, $\alpha_{2,1} = 1.5$. Quasi-extinction level = 5. Results reflect averages from 1000 simulations of 100 years.

4.3.3 Demographic stochasticity with white environmental noise

In this section, we simulate the models with different levels of environmental noise variance σ_e^2, with and without correlation. Demographic stochasticity is always included. We sampled the environmental noise series from a normal distribution with zero mean and variances $\sigma_e^2 \in [0, 1]$ when adding the noise to the growth rate, and $\sigma_e^2 \in [0, 10]$ when adding the noise to the carrying capacity k or directly to the model. We begin by examining the effects of each population's environmental noise variance, with no correlation between the time series. We then compare the quasi-extinction probabilities as functions of time for highly correlated versus uncorrelated environmental noise. Finally, we compare the effects of noise variances for different levels of noise correlation.

4.3.3.1 Uncorrelated noise

We begin by comparing the effects from different variances of uncorrelated white environmental noise in the three competition models. We generate demographic stochasticity based on individual contributions to the demographic growth parameter sampled from a Poisson distribution with mean $\lambda = 1.2$. The unsynchronised white environmental noise is generated from a normal distribution. The noise time series S_1 and S_2 correspond to populations 1 and 2. The competition interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$.

Figure 4.4 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and uncorrelated white environmental noise added to the growth rates λ_1 and λ_2. $(a - c)$ The extinction probabilities $(d - f)$ The average population sizes $(g - i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

Comparing Figures 4.4, 4.5 and 4.6 we notice as in the previous section that including the noise in the model causes the highest extinction risk in the Ricker model, while noise in the growth rate λ_t causes the highest risk in the logistic and Gompertz models. Adding the noise to the carrying capacity k has the smallest total effect, and the least obvious relationships between noise variance and summary metrics.

From the contour plots in Figure 4.4 first row, with increasing the environmental variance the extinction risk tends increases.

Interestingly, in the Gompertz and logistic models with noise added to λ_t (Figure 4.4a and 4.4b), when the weaker population experiences higher environmental variance, it is able to drive the stronger population to extinction and thus ensure its survival. The ability of the stronger population to drive its rival to extinction does not however depend very much on its noise variance - provided the variance of the weaker population's noise is low enough, the stronger population will drive it to extinction and persist. In the Ricker model however, the persistence of either population depends on the variance experienced by *both* populations, with higher variance causing increased persistence(/extinction) for the weaker(/stronger) population.

Changing the variance of the noise when adding it to the carrying capacity causes a relatively minor impact in the distributions of extinction probabilities, the average population sizes and population variances (take note scales in Figure 4.5). Strangely, when the noise is added to the carrying capacity, extinction probabilities for both populations appear to be determined primarily by one population's variance: population 1 in the Gompertz model and population 2 in the Ricker model. the The fact that we having a normal distribution with big variance have great impact on theses distributions, is because of how the carrying capacity is regulating the population size and as such high variance mean high fluctuations and therefore, high risk for both population with no much impact from the interspecific coefficients.

When noise is added to the model (Figure 4.6) we see perhaps the most complex relationships between variances and extinction probabilities, with stark differences between the three models. In the logistic model, extinction probabilities are closely linked, and extinction increases most gradually with variance when the variances are equal (non-equal variances cause extinction at lower amounts of total variance amounts. In the Gompertz model, variance in the noise experienced by population 2 has a stabilising effect on population 1 (likely by controlling the size of population 2), while the variance of population 1 has a destabilizing effect on population 2. In the Ricker model, only the weaker population is at risk of extinction when noise is added directly to the model, and this risk is lower, the higher the environmental variance experienced by the stronger population.

Figure 4.5 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and uncorrelated white environmental noise added to the carrying capacities. $(a-c)$ The extinction probabilities $(d-f)$ The average population sizes $(g-i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.
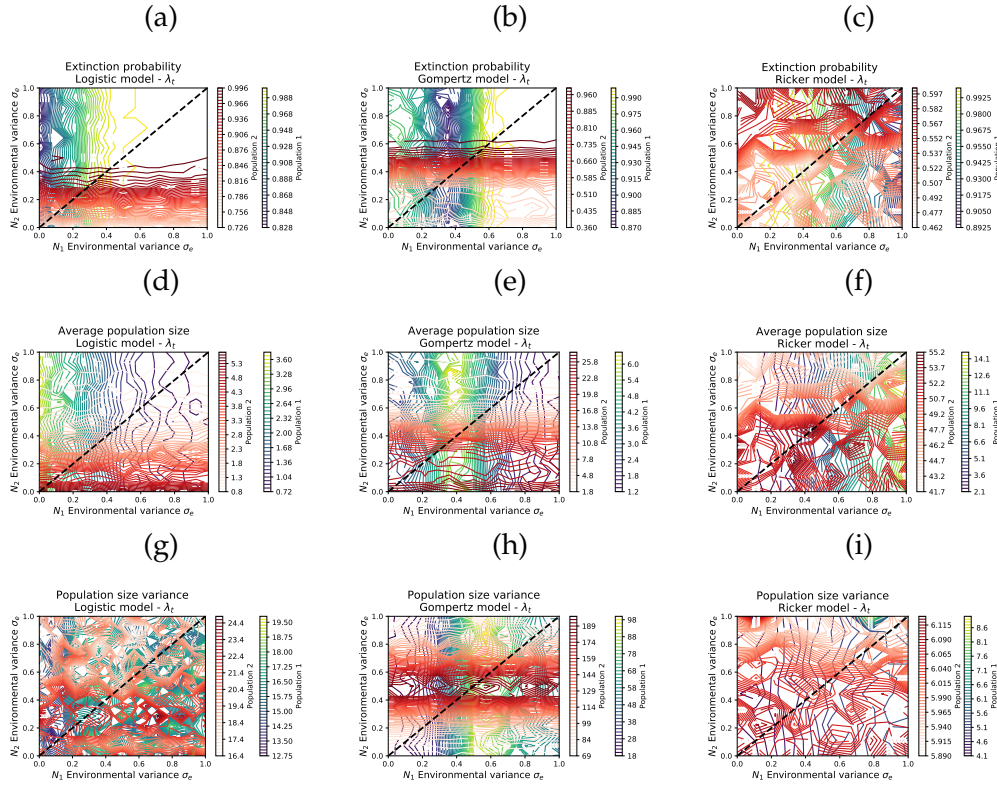
Figure 4.6 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and uncorrelated white environmental noise added to the models. $(a - c)$ The extinction probabilities $(d - f)$ The average population sizes $(g - i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

4.3.3.2 Correlated noise

In this section we compare the effects from different variances of correlated white environmental noise in the three competition models. The goal is to show the rule of the correlated white environmental noise in the population growth and persistence. We generated the demographic stochasticity based on individual fitness values sampled from a Poisson distribution with mean $\lambda = 1.2$. The white environmental noise is generated from a normal distribution. The noise time series S_1 and S_2 correspond to populations 1 and 2. The correlation between the two white environmental noise time se-

ries is $\rho = 0.95$. The competition interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$.

Figure 4.7 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and correlated white environmental noise added to the growth rates λ_1 and λ_2. $(a - c)$ The extinction probabilities $(d - f)$ The average population sizes $(g - i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

Figure 4.8 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and correlated white environmental noise added to the carrying capacities. $(a - c)$ The extinction probabilities $(d - f)$ The average population sizes $(g - i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.
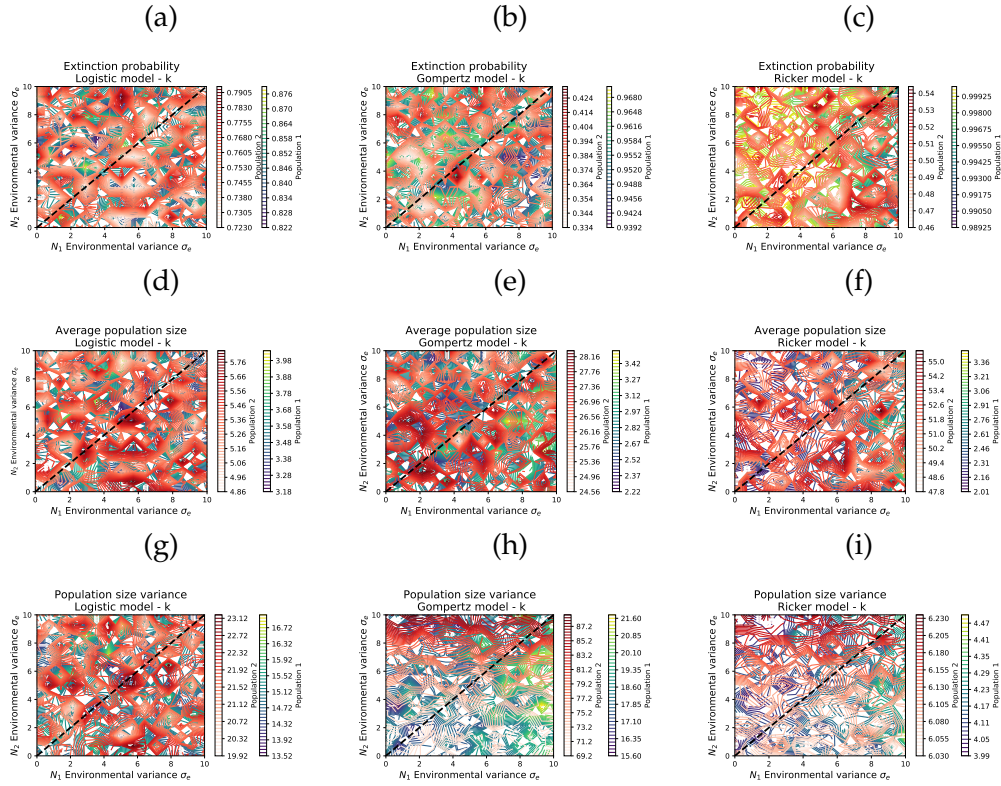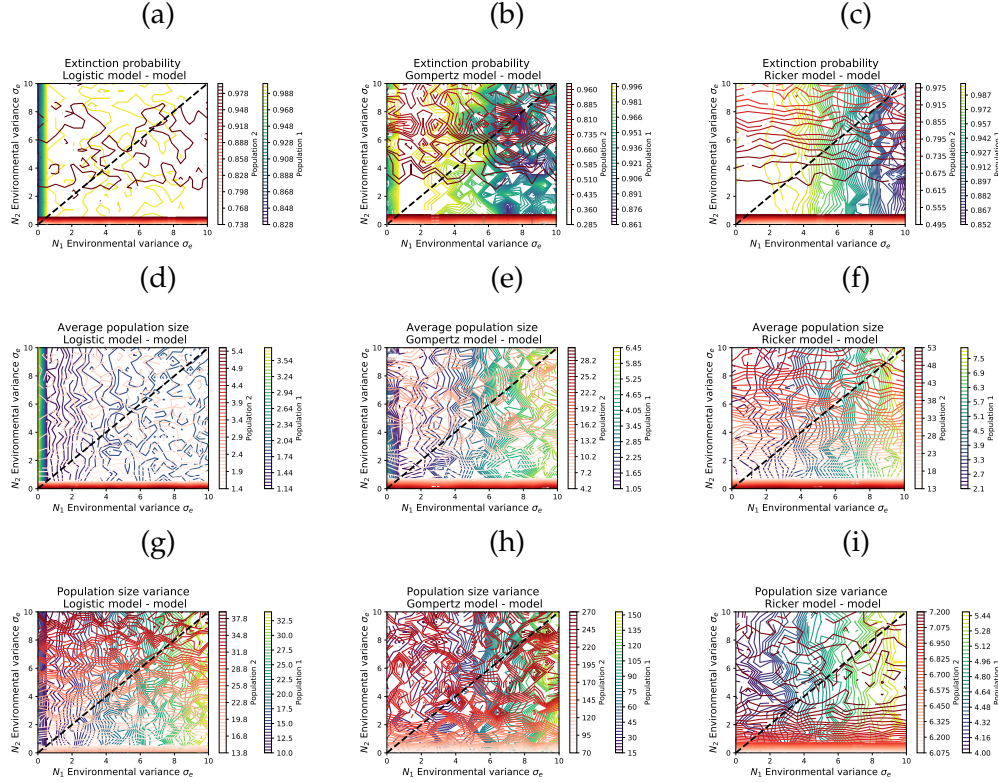
Figure 4.9 – Contour plots of extinction probabilities, the average population sizes and the total population variance as functions of the environmental variance parameter σ_e^2 for logistic, Gompertz and Ricker models with demographic stochasticity and correlated white environmental noise added to the models. $(a - c)$ The extinction probabilities $(d - f)$ The average population sizes $(g - i)$ The variance in the average population sizes. Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

Correlation in the noise added to the growth rates appears to reduce the tolerance of the populations to environmental variance. The results when noise is added to the carrying capacity are even less clear when the noise is correlated. Correlation in the noise added directly to the Gompertz and logistic models causes a distinct qualitative shift (Figure 4.6 b/c vs Figure 4.9 b/c). In the Gompertz model increased chance of extinction for population 2 now occurs for *low* rather than high environmental variance experienced by population 1, while in the logistic model the fates of the two populations are now negatively rather than positively correlated.

4.3.4 Comparing correlation levels

In this section, we explore the effect of different levels of correlation in the environmental time series noises. We simulated the three models, logistic, Gompertz and Ricker with demographic stochasticity and correlated white environmental noise, for 100 years per simulation. We then calculated the extinction probability, the average population size and the total population variance for both populations. The change in the correlation values results in a change in the distribution outcome. We only consider adding the noise in the growth rate λ_t.
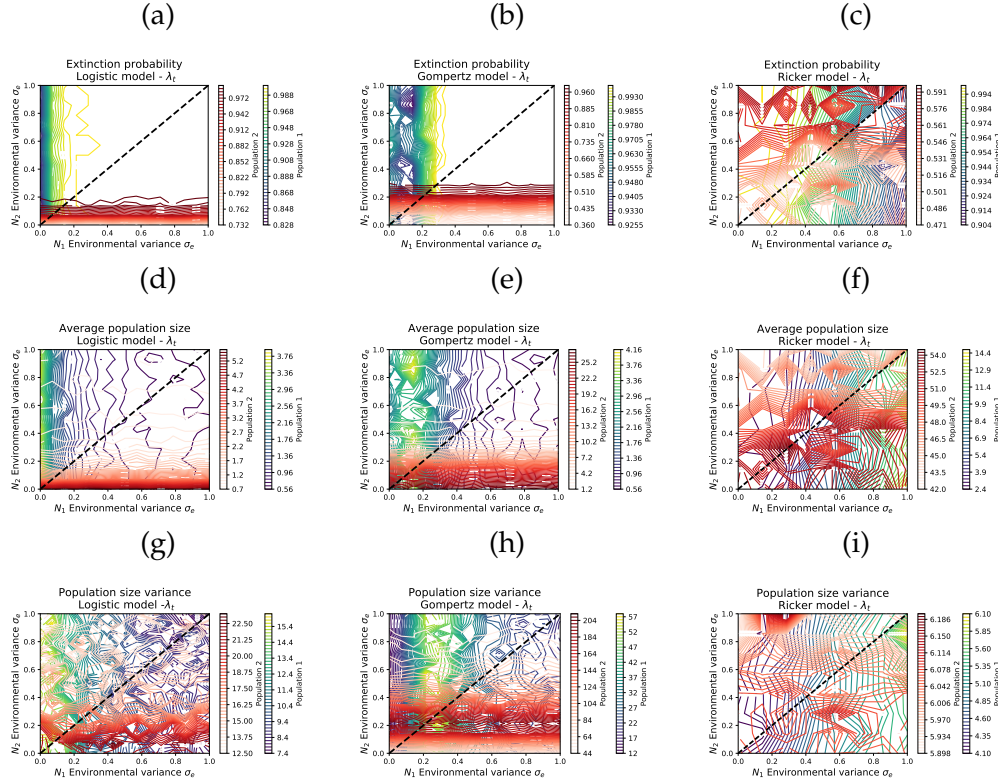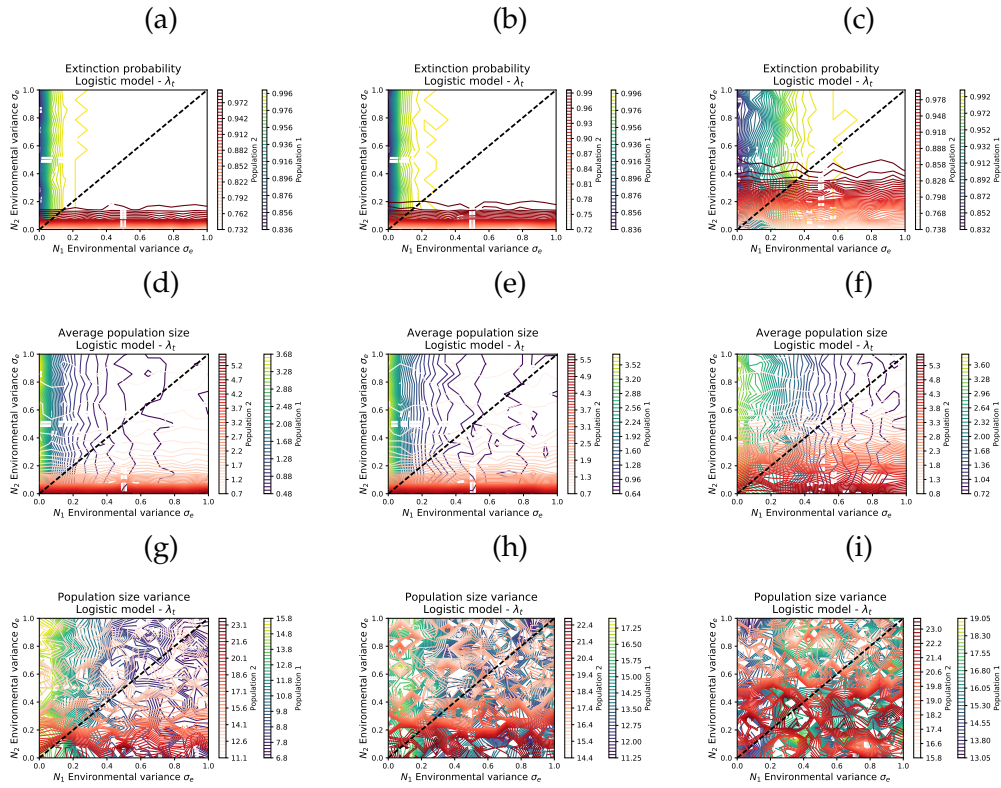

Figure 4.10 – Contour plots of extinction probabilities, average population sizes and total population variances as a functions of the total environmental variances $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$. We are simulating a logistic competition model with demographic stochasticity and correlated white environmental noises. We added the noise to each population of the growth rate. The two white noise time series correlation levels are $\rho = 0.95$ (a, d, g), $\rho = 0.5$ (b, e, h) and $\rho = 0$ (c, f, i). Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the inter-specific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.
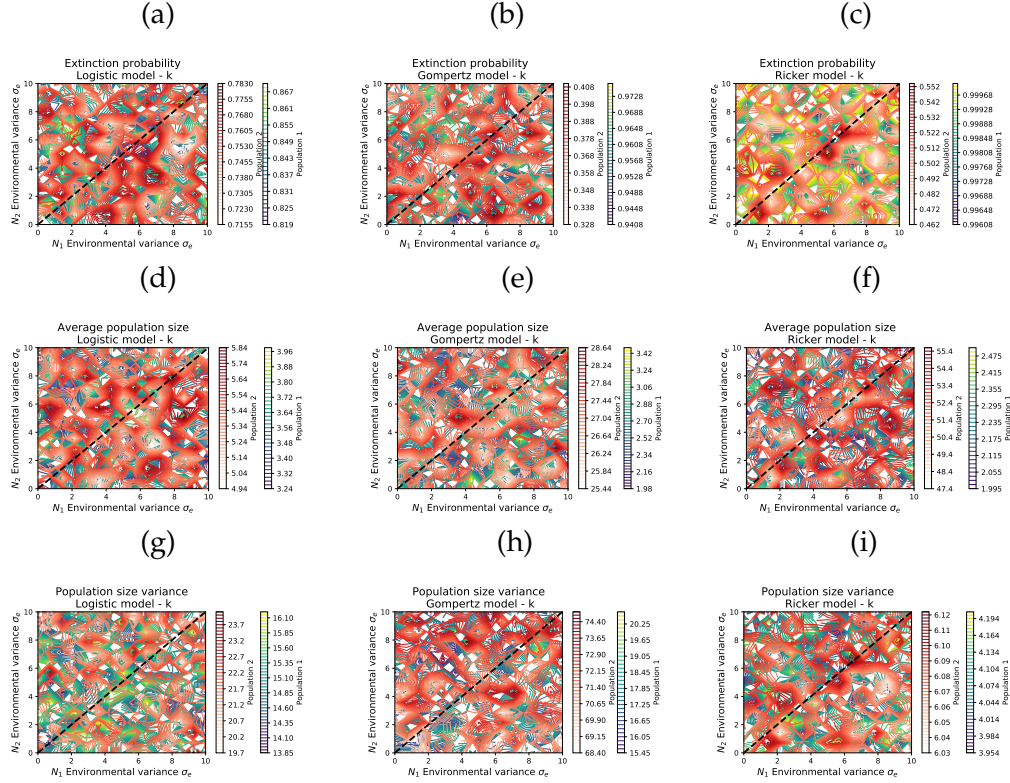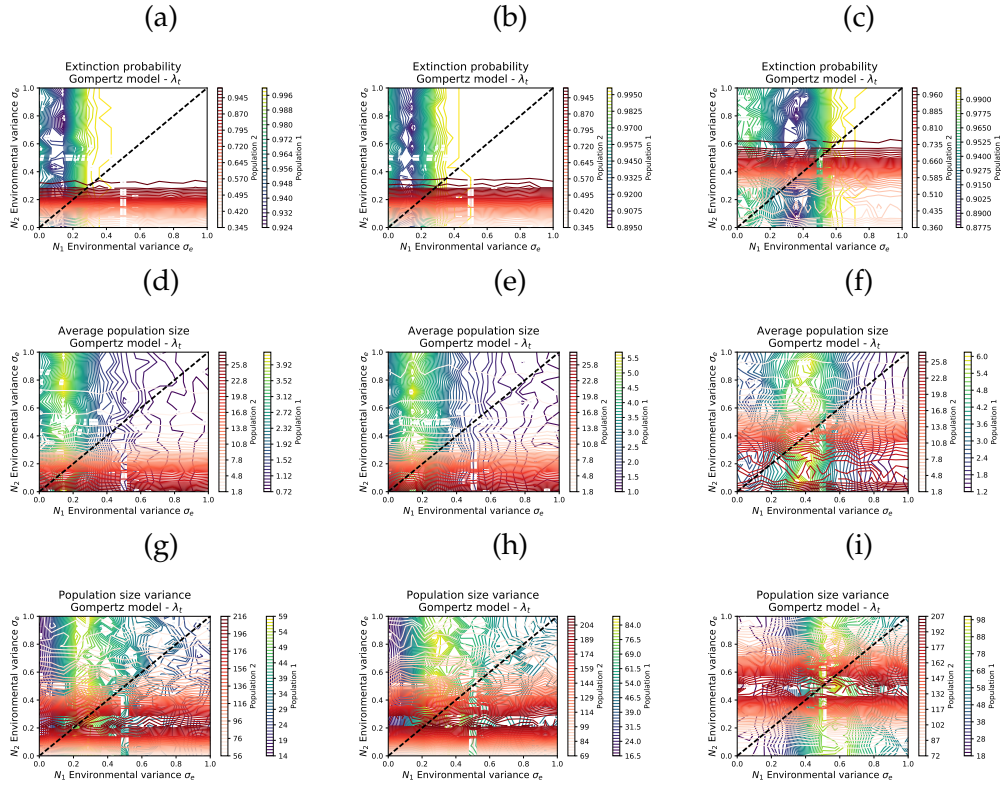
Figure 4.11 – Contour plots of extinction probabilities, average population sizes and total population variances as a functions of the total environmental variances $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$, for Gompertz competition model with demographic stochasticity and correlated white environmental noises added to the population growth rates. The correlation levels between the white noise time series are $\rho = 0.95$ (a, d, g), $\rho = 0.5$ (b, e, h) and $\rho = 0$ (c, f, i). Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.
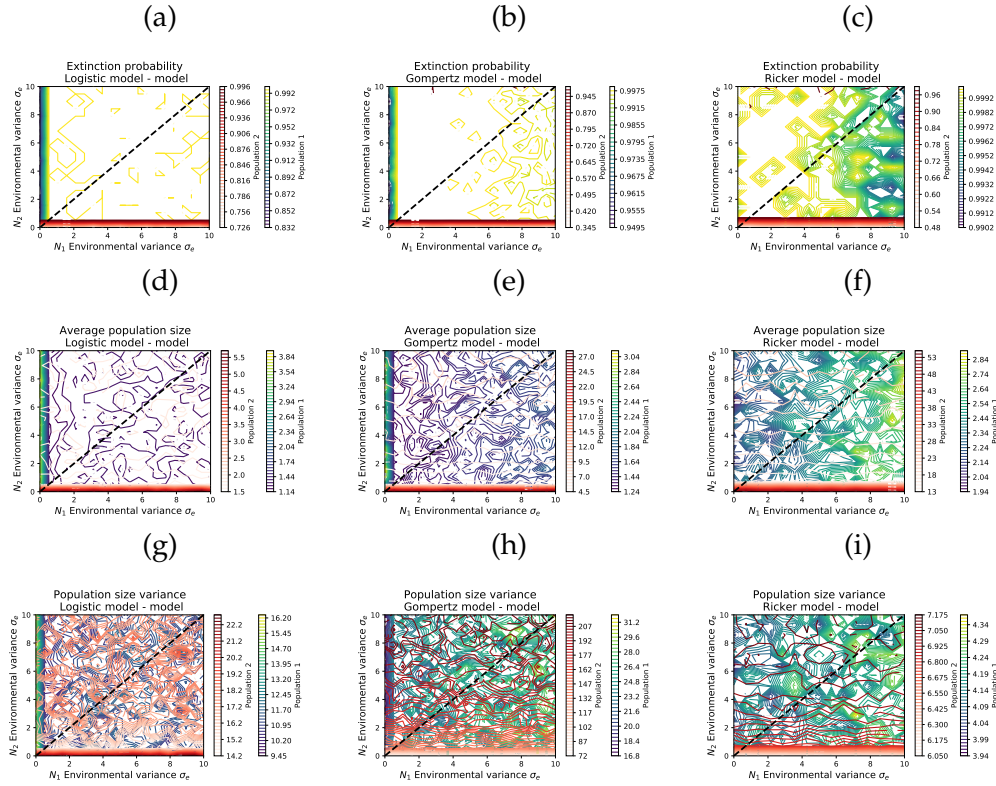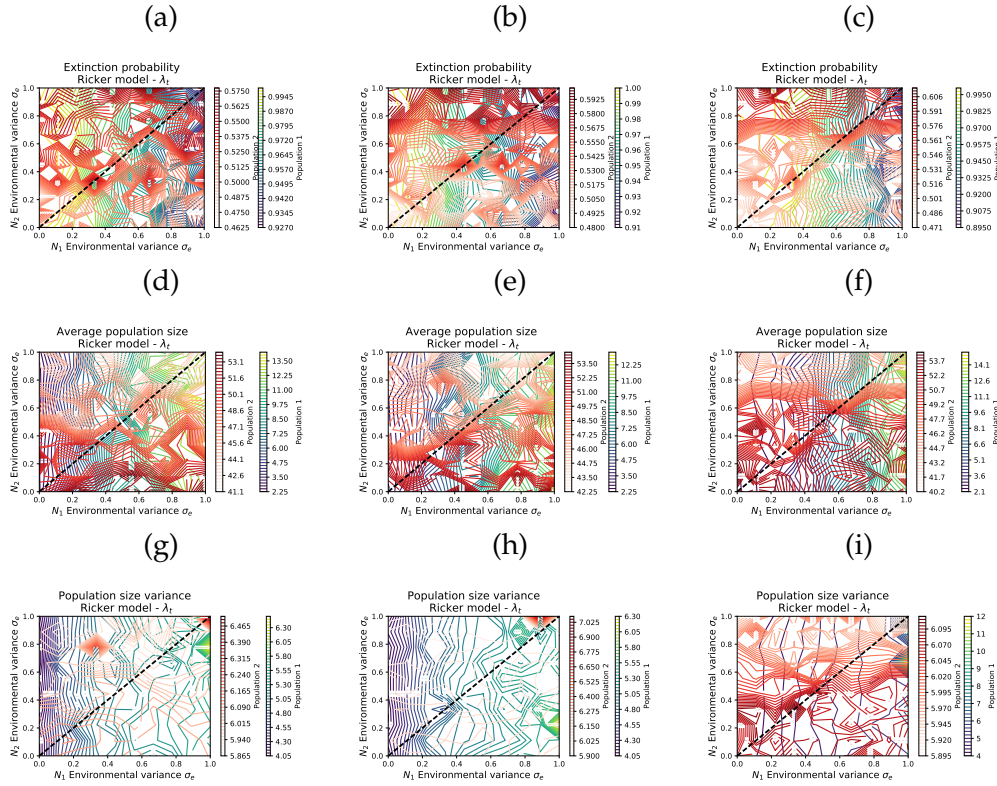
Figure 4.12 – Contour plots of extinction probabilities, average population sizes and total population variances as a functions of the total environmental variances $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$, for Ricker competition model with demographic stochasticity and correlated white environmental noises added to the growth rate. The correlation levels between the white noise time series are $\rho = 0.95$ (a, d, g), $\rho = 0.5$ (b, e, h) and $\rho = 0$ (c, f, i). Initial population sizes are $N_1 = N_2 = 10$, carrying capacities are $k_1 = k_2 = 100$ and the interspecific interaction coefficients are $\alpha_{1,2} = 1.1$ and $\alpha_{2,1} = 1.5$. Plots reflect averages from 1000 realisations of 100 years for each λ_1 / λ_2 combination.

In the logistic and Gompertz models, correlation in the noise reduces the tolerance of populations to the total variance, presumably via the same mechanism discussed in Section 4.3.3.2.

In the Ricker model, an odd reversal of dependencies occurs when even moderate correlation appears in the noise. Regions with the least/most (population 1/2) extinction risk occur with uncorrelated noise on the sides of the plots, i.e. when one variance is low and the other high (Figure 4.12a). With correlated noise, the lowest/highest (population 1/2) extinction risk occurs in the upper right hand corner, when both variances are large. The reason for this shift are not clear.

Chapter 5

Conclusion

In this work, we studied the behaviour of single and two population stochastic logistic, Gompertz and Ricker models, focussing on outcomes related to extinction risk. We examined the effects of two broad types of stochasticity. We explored the effects of various environmental noise colours, total environmental noise variance, and environmental noise correlation, comparing within and between noise "locations" in the model. We also explored the effects of changing the Poisson parameter(s) from which individual contributions to the demographic growth parameters are sampled.

We found across all the models that adding the noise into the growth parameter λ_t has a large effect in the probability distributions of extinction risk. However, the effects of demographic stochasticity are small once population sizes become large.

There is an ongoing debate in the field of PVA modelling as to whether noise colour contributes to or detracts from extinction risk. We found that coloured noise generally causes a slight decrease in the extinction risk. Including environmental noise in the models influences the population dynamics, for instance, increasing the variance of the environmental noise increases the extinction risk. The Ricker model has high persistence rate and logistic model has the highest extinction risk.

We found that correlation between environmental noise for two populations generally increases the extinction risk. Conservationists might consider developing methods through which to reduce the correlation of environmental noise effects on different species. Bear in mind that we have only explored the effects of *one* type of environmental noise correlation/non-correlation - that is, through totally random effects. As is usually the case

with the development of an area of modelling interest, there is much room for expert contribution and specific tailoring of this model to explore other types of non-correlation (for example, including damping of the effects on one population, or negative correlation).

A number of effects observed are somewhat counter-intuitive, and warrant further investigation. We suggest that such investigation focus on the particular paths to extinction (e.g. simultaneous population booms) determining the dynamics in each scenario. In addition, future work should relate the findings presented in this work with real-world data and management options.

Model choice is a crucial decision when performing PVA's to inform management decisions. Indeed, in many cases the models examined here could suggest very different management strategies, with potentially disastrous results should a model be inappropriately chosen. Model selection falls outside the scope of his work, but we refer readers to [1, 33] for a review of the topic.

We conducted a comprehensive set of simulations to investigate the implications of model choice, incorporation of stochasticity, parametric assumptions and noise quality for Population Viability Analyses. Our work contributes to ongoing debates regarding noise colour and correlation, and provides valuable information regarding the sensitivity of extinction outcomes to various modelling assumptions.

Appendices

Appendix A

A.1 Glossary

A.1.1 Stochasticity

Stochasticity is any event characterized by random chance or a random probability distribution. In ecological communities, stochasticity is the noise that interacts with the population dynamics. The scale and type of noise is determined by the population density and ecological behaviour for each species in the population.

A.1.2 Correlation

A correlation is a measure of a linear association between two random variables. The correlation is always in a range $[-1, 1]$; stronger when its closer to ± 1.

A.1.3 Autocorrelation

The autocorrelation is a correlation between the time series and its own past. The 'value' of a time-series autocorrelation depends on the time separation for which it is calculated.

A.1.4 Coloured noise

Coloured noise refers to noise with non-zero temporal autocorrelation structure. White noise is uncorrelated in time, so that future environmental conditions do not depend on past environmental conditions. The variations in environmental conditions represented by different coloured noise, red

or pink noises, when the environment vary slower and they have positive correlation. Blue noise, the environment vary faster, and it has negative correlation.

A.2 Simple model of stochastic population growth

The main goal of modelling dynamics of any populations is to understand how population size changes through time, and how these changes are results of a crucial factors for example, the environmental (whether biotic or abiotic) and demographic elements.

Here we examine a population that grows in discrete time segments, with non-overlapping generations. Suppose $i_1, i_2, ..., i_N$ represent individual fitness values, which we define as the individual contributions to the population at time $t + 1$ (including both reproduction and/or survival). Suppose that this individual contribution is distributed with a mean $\mu(N_t, e_t)$ and variance $\sigma^2(N_t, e_t)$ that depend on the population size N_t and environmental state e_t. Therefore, the growth of the future population N_{t+1} will be depend on the past population N_t, and on the environmental conditions at time t, mathematically would be represented by,

$$N_{t+1} = i_1 + i_2 + ... + i_N, \tag{A.1}$$

The expected population on the next generation is:

$$E[N_{t+1}|N_t, e_t] = E[i_1 + i_2 + ... + i_N] = \mu(N_t, e_t)N_t, \tag{A.2}$$

This is a simple example of stochastic population model represented by the mean and variance of demographic and environmental factors. Where μ is representing the growth rate. This is an example of a stochastic density dependent growth model.
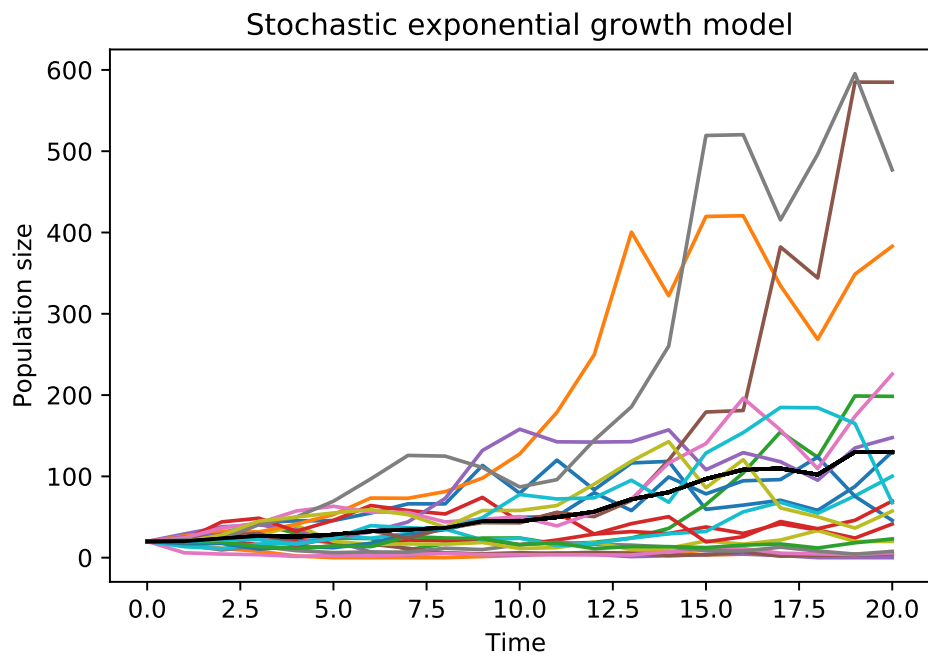
Figure A.1 – A simulation of stochastic exponential growth model. The initial population one size = 20, the environmental noise generated form normal distribution with zero mean and variance one, the black curve is the average exponential growth.

Appendix B

Summary of variables used

Below is a list of the various variables used in this work.

Table B.1 – Summary of variables used

Symbol	Meaning
σ_e^2	Environmental variance
σ_d^2	Demographic variance
QEL	Quasi extinction level
E_p	Extinction probability
CDF	Cumulative distribution function
MTE	Mean time to extinction
PSD	Power spectral density
ρ	Correlation coefficient

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