

Demographic stochasticity

Disease spread in populations of individuals

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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US-Africa Advanced Study Institute on Mathematical Modeling of Infectious Diseases in Africa June 2007

Notes

- The printed notes are meant to assist you only

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Notes

- The printed notes are meant to assist you only
- They are incomplete

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Notes

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The printed notes are meant to assist you only
- They are incomplete
 - ◆ In fact, I have no idea what they say

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Introduction

Modelling individual events

- Differential equations model continuous processes

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Modelling individual events

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Differential equations model continuous processes
- Disease spreads in the real world through discrete events

Modelling individual events

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Differential equations model continuous processes
- Disease spreads in the real world through discrete events
- Discrete events are fundamentally stochastic

Modelling individual events

● Demographic stochasticity

Introduction

● **Modelling individual events**

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Differential equations model continuous processes
- Disease spreads in the real world through discrete events
- Discrete events are fundamentally stochastic
 - ◆ Even in theory we don't know when the next event will occur, nor even what it will be

Types of stochasticity

- Demographic stochasticity is caused by the existence of individual people and discrete events

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Types of stochasticity

- Demographic stochasticity is caused by the existence of individual people and discrete events
- Environmental stochasticity refers to events that affect more than one person at a time

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Types of stochasticity

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Demographic stochasticity is caused by the existence of individual people and discrete events
- Environmental stochasticity refers to events that affect more than one person at a time
 - ◆ Weather

Types of stochasticity

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Demographic stochasticity is caused by the existence of individual people and discrete events
- Environmental stochasticity refers to events that affect more than one person at a time
 - ◆ Weather
 - ◆ Politics

Types of stochasticity

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Demographic stochasticity is caused by the existence of individual people and discrete events
- Environmental stochasticity refers to events that affect more than one person at a time
 - ◆ Weather
 - ◆ Politics
 - ◆ Economics

Modelling individual events

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



A stochastic potential-transmission event

Deterministic spread

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

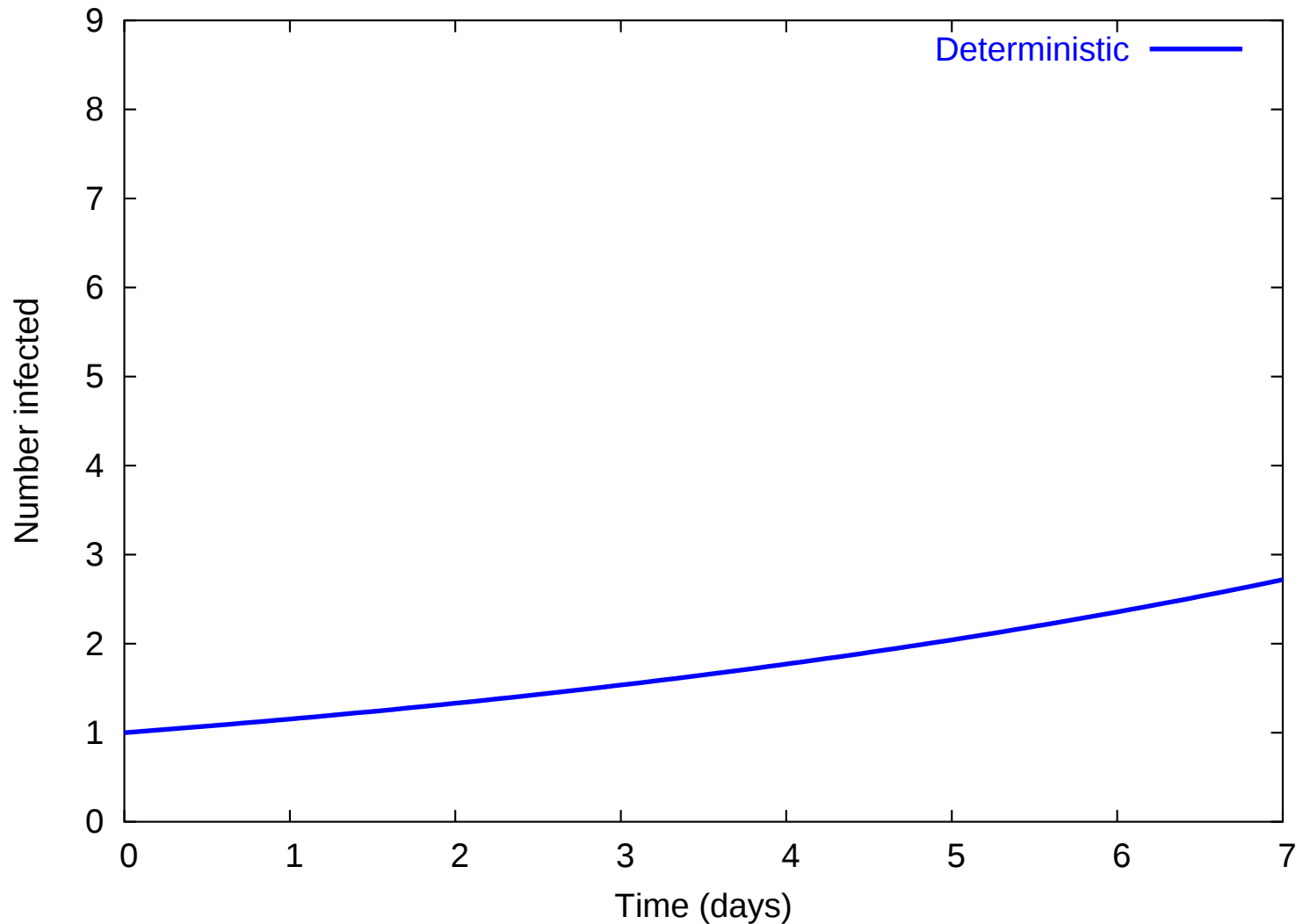
Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



Demographic spread

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

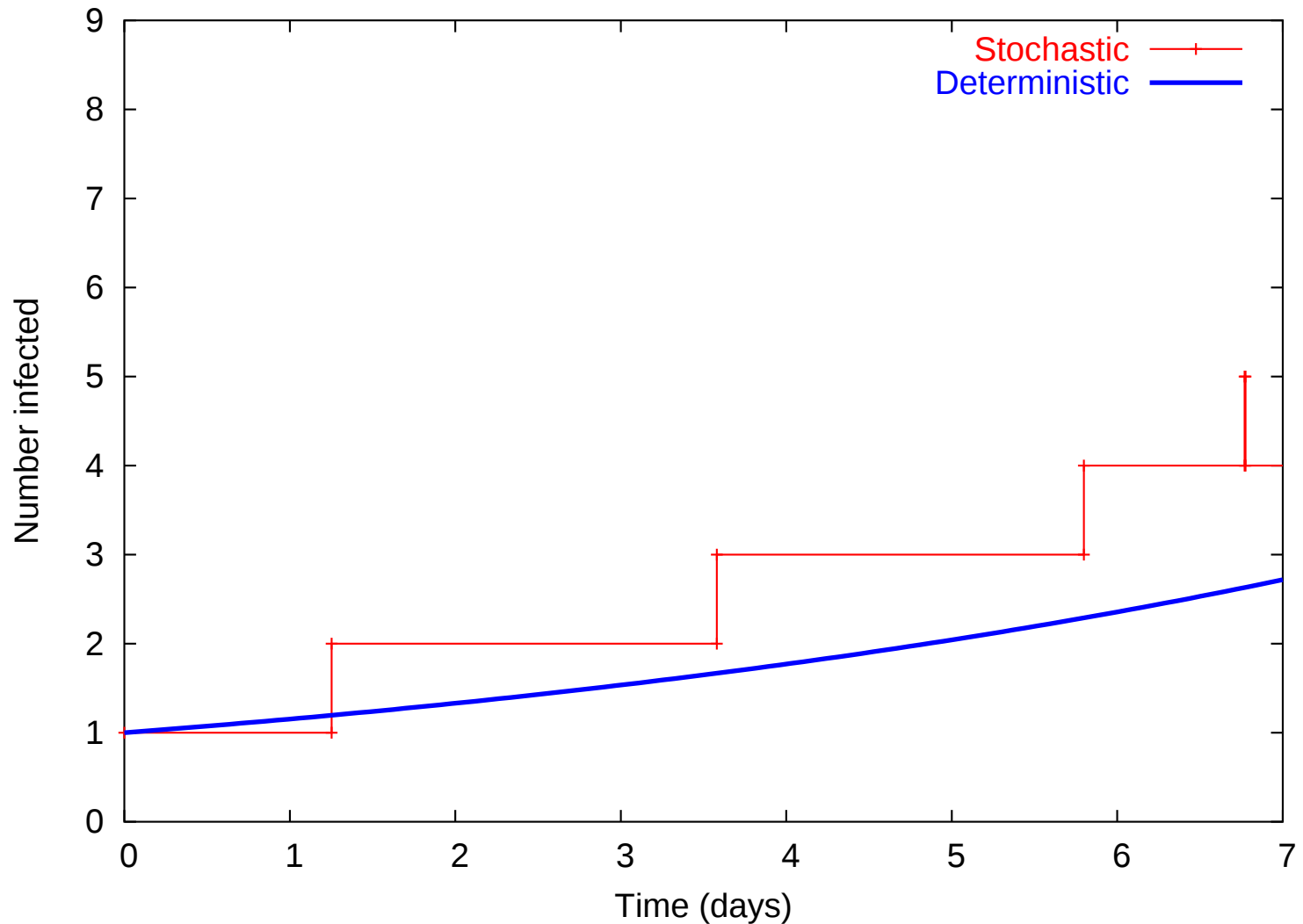
Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



Demographic spread

● Demographic stochasticity

Introduction

● Modelling individual events

● Types of stochasticity

Describing a stochastic process

Equilibrium and quasi-equilibrium

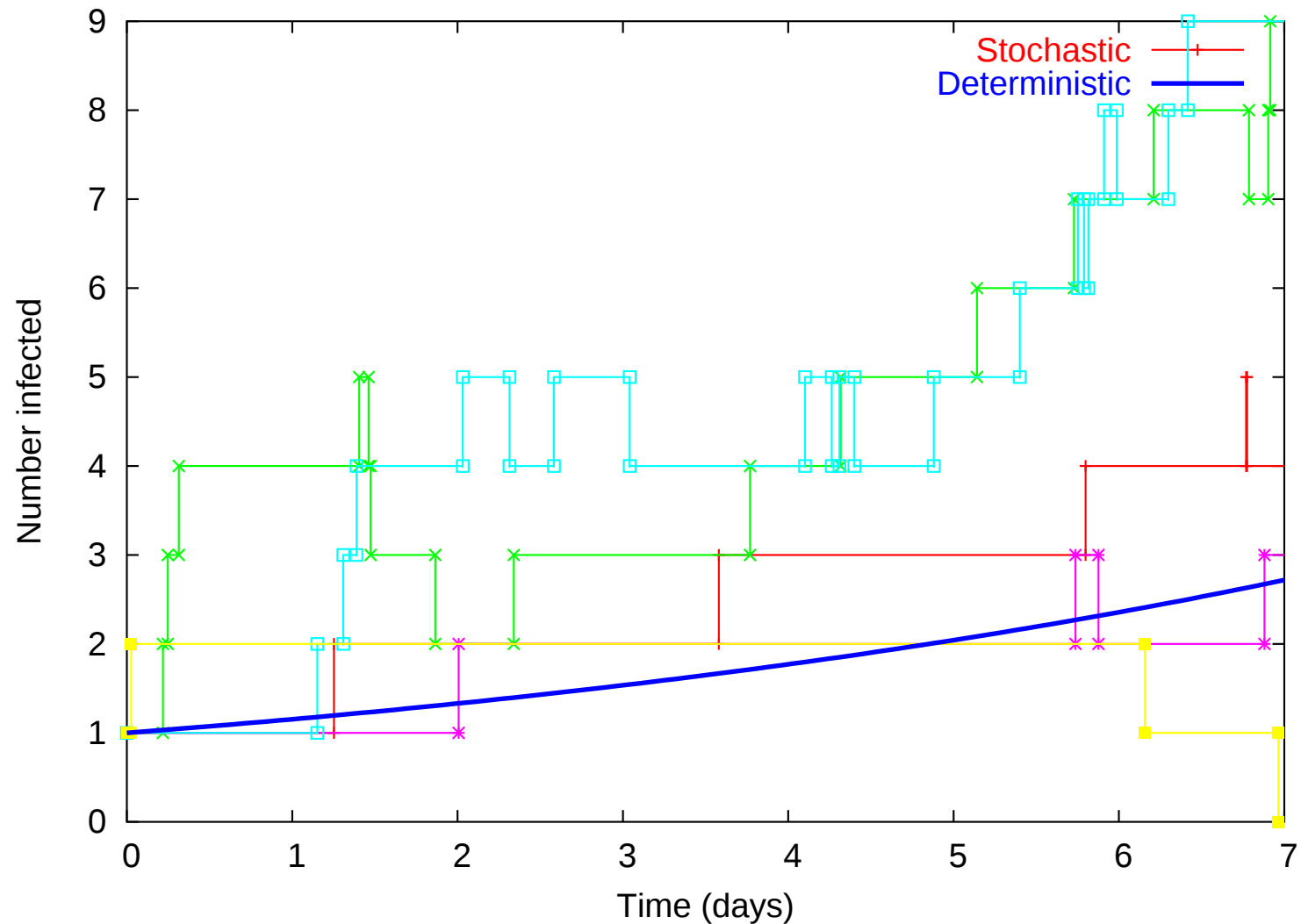
Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



● Demographic stochasticity

Introduction

Describing a stochastic process

- States and rates
- Realizations and ensembles
- Simulating a realization
- Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Describing a stochastic process

States and rates

- We describe our system in terms of the *probability rates* of events happening

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

States and rates

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We describe our system in terms of the *probability rates* of events happening
 - ◆ If the rate of event E is $r_E(t)$, the probability of the event occurring in the time interval $(t, t + dt)$ is $r_E(t)dt$

States and rates

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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States and rates

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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 - ◆ The Markovian assumption is *extremely* convenient, but can have unwanted consequences

States and rates

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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 - ◆ If the rate of event E is $r_E(t)$, the probability of the event occurring in the time interval $(t, t + dt)$ is $r_E(t)dt$
- If the system is *Markovian*, $r_E(t)$ depends only on the state of the system at time t
 - ◆ The Markovian assumption is *extremely* convenient, but can have unwanted consequences
- If the system is *non-Markovian* $r_E(t)$ can depend (for example) on how long the system has been in a particular state

States and rates (Deterministic)

- Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

- Realizations and ensembles
- Simulating a realization
- Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

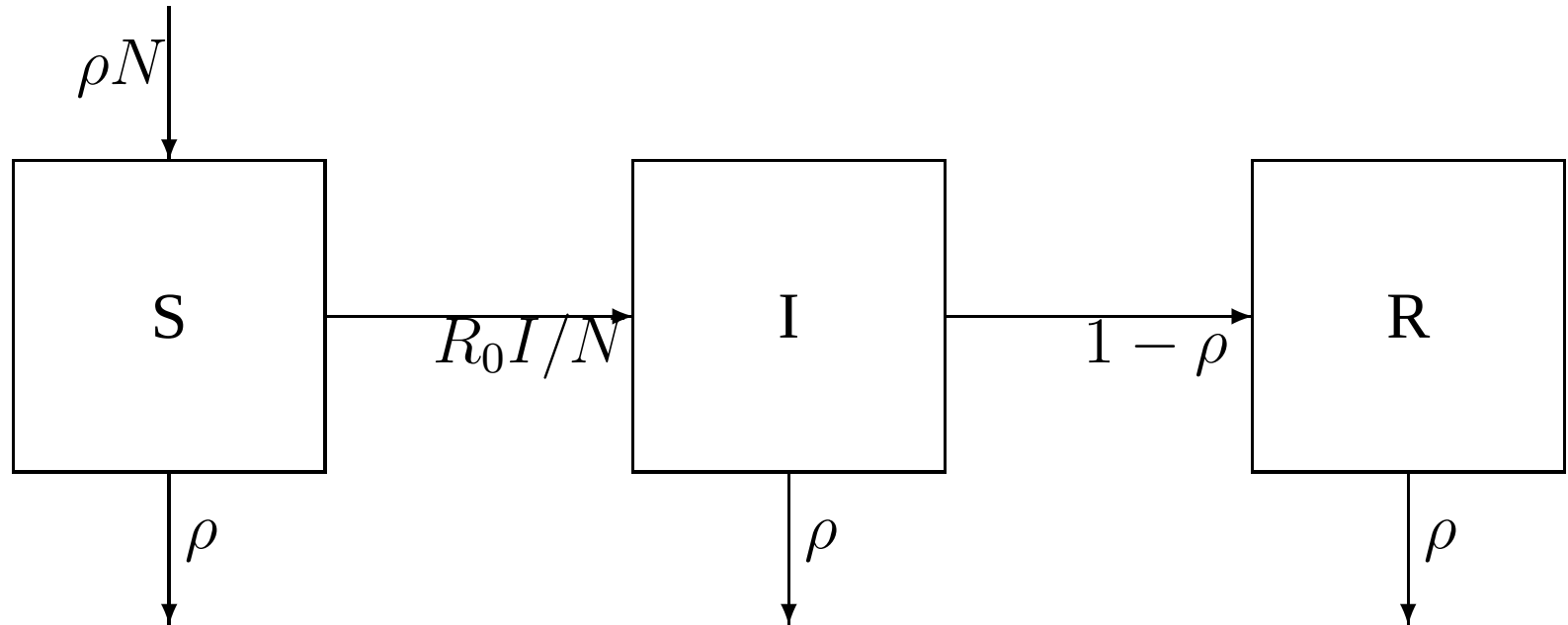
Simulating distributions

Simulating realizations

Strain interactions

Conclusions

SIR model with birth and death



$$\begin{aligned}\dot{S} &= \rho(N - S) - R_0 SI / N \\ \dot{I} &= R_0 SI / N - I\end{aligned}$$

States and rates (Demographic)

- Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

- Realizations and ensembles
- Simulating a realization
- Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

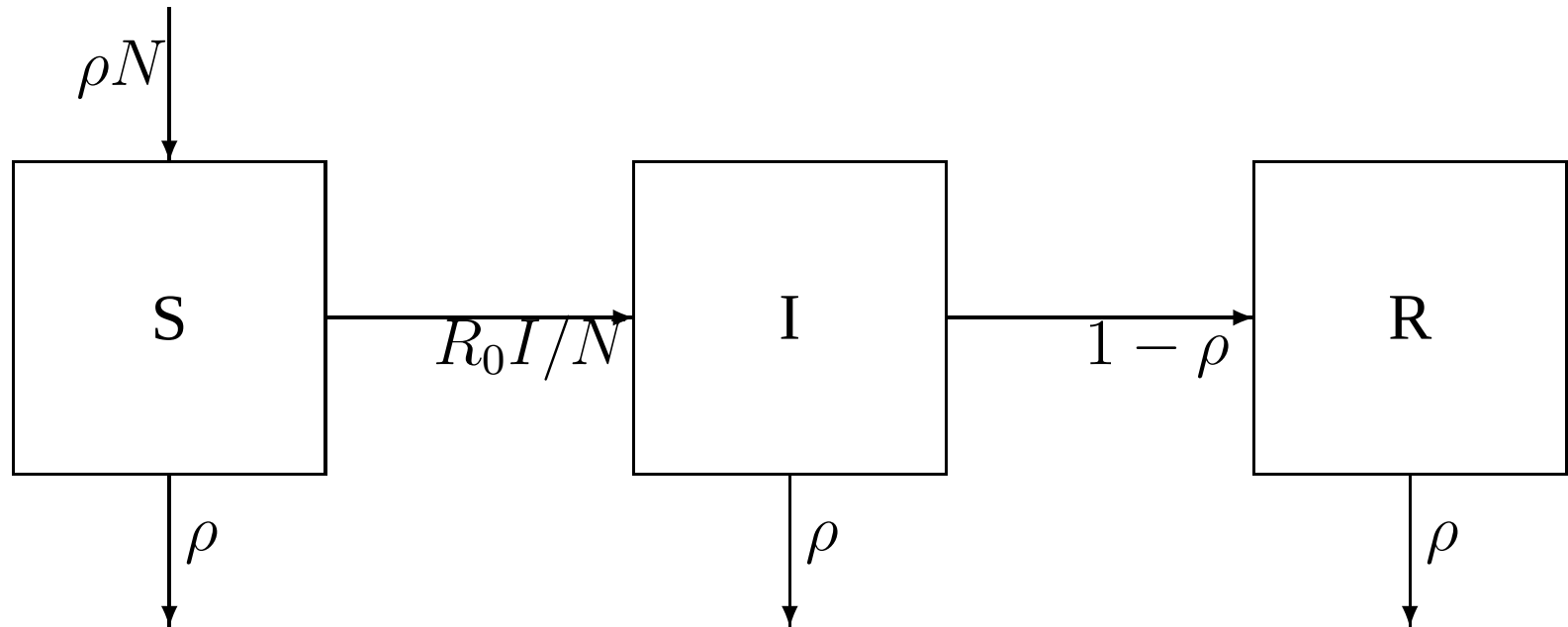
Simulating distributions

Simulating realizations

Strain interactions

Conclusions

SIR model with birth and death



Event	transition	rate
Infection	$S \rightarrow I$	$R_0 SI/N$
Recovery	$I \rightarrow R$	$(1 - \rho)I$
Rebirth	$R \rightarrow S$	ρR
Rebirth	$I \rightarrow S$	ρI

Analogy

- The demographic model is an exact analogue of the deterministic one

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Analogy

- The demographic model is an exact analogue of the deterministic one
 - ◆ Conceptually

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Analogy

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The demographic model is an exact analogue of the deterministic one
 - ◆ Conceptually
 - ◆ In the limit as $N \rightarrow \infty$

Analogy

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The demographic model is an exact analogue of the deterministic one
 - ◆ Conceptually
 - ◆ In the limit as $N \rightarrow \infty$
- Choices may be required

Analogy

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The demographic model is an exact analogue of the deterministic one
 - ◆ Conceptually
 - ◆ In the limit as $N \rightarrow \infty$
- Choices may be required
 - ◆ Should we include stochasticity in population size?

Realizations and ensembles

- How do we think about the behavior of a stochastic process?

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Realizations and ensembles

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- How do we think about the behavior of a stochastic process?
 - ◆ A single example of how the process could go (e.g., from a stochastic simulation) is called a *realization*

Realizations and ensembles

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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 - ◆ The universe of possible realizations is called the *ensemble*.

Realizations and ensembles

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization
● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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 - ◆ A single example of how the process could go (e.g., from a stochastic simulation) is called a *realization*
 - ◆ The universe of possible realizations is called the *ensemble*.
 - ◆ The probability distribution that describes what state we expect the population to be in at time t is called the *ensemble distribution*

Realizations and ensembles

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- How do we think about the behavior of a stochastic process?
 - ◆ A single example of how the process could go (e.g., from a stochastic simulation) is called a *realization*
 - ◆ The universe of possible realizations is called the *ensemble*.
 - ◆ The probability distribution that describes what state we expect the population to be in at time t is called the *ensemble distribution*
 - Knowing how the ensemble distribution evolves is not the same as understanding the whole ensemble

Some techniques

■ Simulate one or many realizations

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Some techniques

- Simulate one or many realizations
- Simulate the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Some techniques

- Simulate one or many realizations
- Simulate the ensemble distribution
 - ◆ Requires one state variable for each possible state of the system

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Some techniques

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates

● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Simulate one or many realizations
- Simulate the ensemble distribution
 - ◆ Requires one state variable for each possible state of the system
- Solve the ensemble distribution dynamics exactly!

Some techniques

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization
● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Simulate one or many realizations
- Simulate the ensemble distribution
 - ◆ Requires one state variable for each possible state of the system
- Solve the ensemble distribution dynamics exactly!
 - ◆ Rarely possible

Some techniques

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization
● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Simulate one or many realizations
- Simulate the ensemble distribution
 - ◆ Requires one state variable for each possible state of the system
- Solve the ensemble distribution dynamics exactly!
 - ◆ Rarely possible
- Analytic approximations to the ensemble distribution

Simulating a realization

- Given a state of the system:

- Demographic stochasticity

Introduction

Describing a stochastic process

- States and rates
- Realizations and ensembles
- **Simulating a realization**
- Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Simulating a realization

- Given a state of the system:
 - ◆ List possible events, and associated rates

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● **Simulating a realization**

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● **Simulating a realization**

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
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 - ◆ The probability of event E is r_E/r_T

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
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 - ◆ The probability of event E is r_E/r_T
 - ◆ Randomly select the time and nature of the next event

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● **Simulating a realization**

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
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 - ◆ The probability of event E is r_E/r_T
 - ◆ Randomly select the time and nature of the next event
 - ◆ Change the system state appropriately

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
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 - ◆ Change the system state appropriately
 - ◆ Repeat forever

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Repeat forever
 - Or until system is extinct

Conclusions

Simulating a realization

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Given a state of the system:
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 - ◆ Change the system state appropriately
 - ◆ Repeat forever
 - Or until system is extinct
 - Or until you are tired

Deterministic model

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● **Simulating a realization**

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

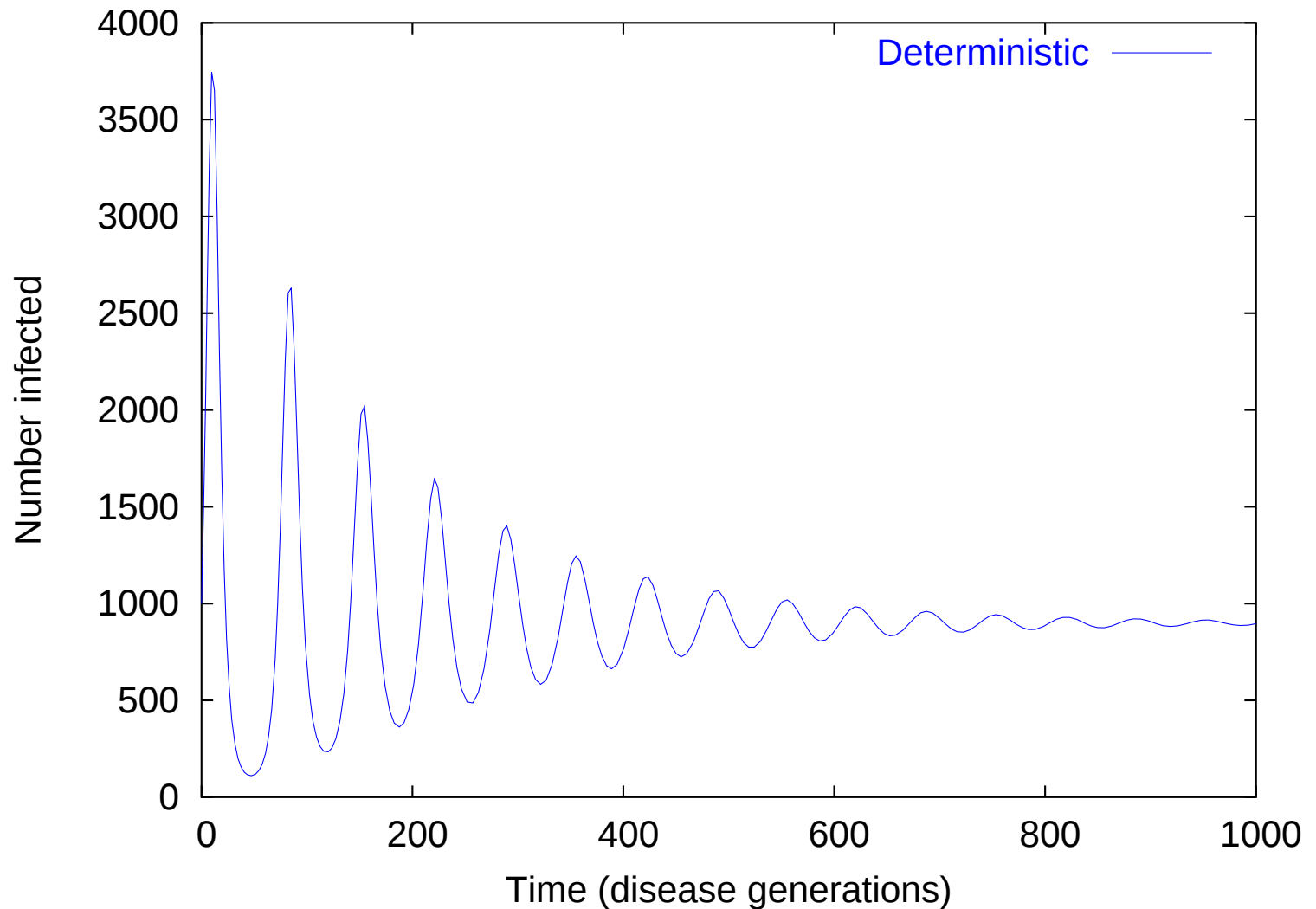
Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



Demographic model

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles

● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

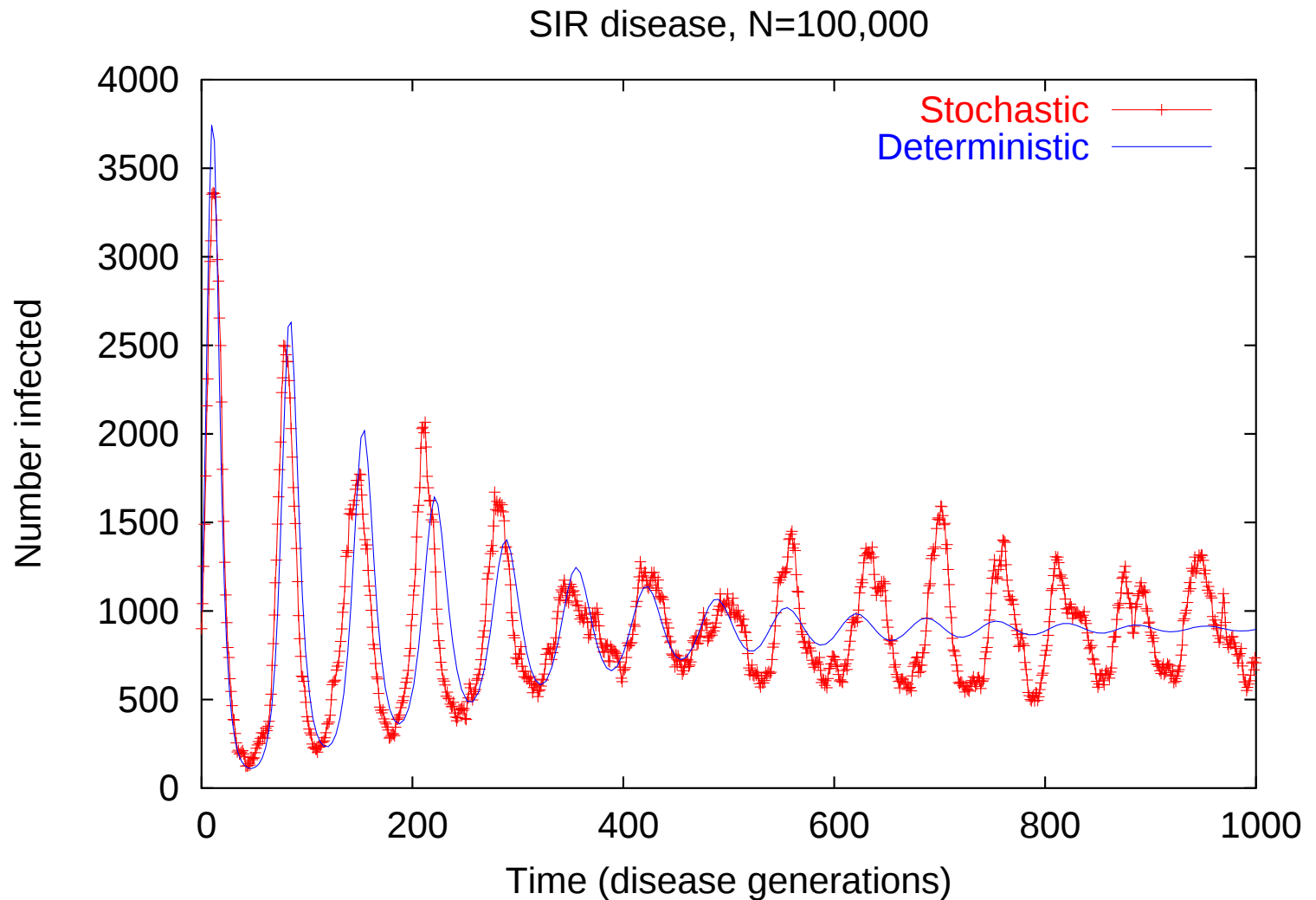
Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions



Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We model the ensemble distribution by creating one conceptual ‘box’ for each possible state of the system, and asking what is the probability that the system is in each box.

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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- The probabilities change as follows:

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

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- ◆ This can be a lot of boxes

- The probabilities change as follows:

- $$\dot{p}_S = \sum_{S'} p_{S'} r_{S' \rightarrow S} - p_S \sum_{S'} r_{S \rightarrow S'}$$

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution
- We might seek to solve these equations analytically

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution
- We might seek to solve these equations analytically
 - ◆ Only in special cases

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution
- We might seek to solve these equations analytically
 - ◆ Only in special cases
- We might seek analytic approximations to increase our understanding

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution
- We might seek to solve these equations analytically
 - ◆ Only in special cases
- We might seek analytic approximations to increase our understanding
 - ◆ Moment approximations

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- If our system is small enough (particularly, if it has one state dimension) we might be able to simulate the ensemble distribution
- We might seek to solve these equations analytically
 - ◆ Only in special cases
- We might seek analytic approximations to increase our understanding
 - ◆ Moment approximations
 - ◆ Diffusion approximations

Questions

- What kind of questions do we want to ask with a stochastic model?

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● **Modelling the ensemble distribution**

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?
 - Spatial distribution

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?
 - Spatial distribution
 - Establishment

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?
 - Spatial distribution
 - Establishment
 - Persistence

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?
 - Spatial distribution
 - Establishment
 - Persistence
 - ◆ How much variance do we expect stochasticity to cause?

Questions

● Demographic stochasticity

Introduction

Describing a stochastic process

● States and rates
● Realizations and ensembles
● Simulating a realization

● Modelling the ensemble distribution

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- What kind of questions do we want to ask with a stochastic model?
 - ◆ How does stochasticity affect disease dynamics?
 - Spatial distribution
 - Establishment
 - Persistence
 - ◆ How much variance do we expect stochasticity to cause?
 - ◆ Under what circumstances can we eliminate or eradicate a disease?

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium
● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Equilibrium and quasi-equilibrium

Equilibrium

- Define equilibrium as an ensemble distribution that does not change with time

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?
 - ◆ Disease free equilibrium

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?
 - ◆ Disease free equilibrium
 - ◆ Others?

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?
 - ◆ Disease free equilibrium
 - ◆ Others?
- There is no equilibrium corresponding to the endemic equilibrium of the deterministic system!

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?
 - ◆ Disease free equilibrium
 - ◆ Others?
- There is no equilibrium corresponding to the endemic equilibrium of the deterministic system!
 - ◆ As long as any populations not extinct, proportion extinct will increase.

Equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Define equilibrium as an ensemble distribution that does not change with time
- What are the equilibria of our stochastic SIR system?
 - ◆ Disease free equilibrium
 - ◆ Others?
- There is no equilibrium corresponding to the endemic equilibrium of the deterministic system!
 - ◆ As long as any populations not extinct, proportion extinct will increase.
 - ◆ This is deeply inconvenient

Quasi-equilibrium

- Consider the ensemble distribution confined to the subset of states where nothing is extinct

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Consider the ensemble distribution confined to the subset of states where nothing is extinct
- This system can be described as a *fully connected* (you can get anywhere from anywhere else, *open* (you can leave the set) flow.

Quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Consider the ensemble distribution confined to the subset of states where nothing is extinct
- This system can be described as a *fully connected* (you can get anywhere from anywhere else, *open* (you can leave the set) flow.
 - ◆ Intuition tells us that such a system has a unique, real, negative dominant eigenvalue, associated with a positive eigenvector

Quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Consider the ensemble distribution confined to the subset of states where nothing is extinct
- This system can be described as a *fully connected* (you can get anywhere from anywhere else, *open* (you can leave the set) flow.
 - ◆ Intuition tells us that such a system has a unique, real, negative dominant eigenvalue, associated with a positive eigenvector
 - Linear algebra tells us this as well

Quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Consider the ensemble distribution confined to the subset of states where nothing is extinct
- This system can be described as a *fully connected* (you can get anywhere from anywhere else, *open* (you can leave the set) flow.
 - ◆ Intuition tells us that such a system has a unique, real, negative dominant eigenvalue, associated with a positive eigenvector
 - Linear algebra tells us this as well
 - ◆ *What does this mean?*

Quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Consider the ensemble distribution confined to the subset of states where nothing is extinct
- This system can be described as a *fully connected* (you can get anywhere from anywhere else, *open* (you can leave the set) flow.
 - ◆ Intuition tells us that such a system has a unique, real, negative dominant eigenvalue, associated with a positive eigenvector
 - Linear algebra tells us this as well
 - ◆ *What does this mean?*
 - System will converge to a stable *relative* distribution of probabilities of being in each non-extinct box

Interpreting the quasi-equilibrium

- The quasi-equilibrium is the asymptotic distribution of system states given that nothing has gone extinct

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Interpreting the quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The quasi-equilibrium is the asymptotic distribution of system states given that nothing has gone extinct
- The eigenvalue λ_q associated with the quasi-equilibrium distribution is the rate at which the probability of non-extinction decays (exponentially)

Interpreting the quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The quasi-equilibrium is the asymptotic distribution of system states given that nothing has gone extinct
- The eigenvalue λ_q associated with the quasi-equilibrium distribution is the rate at which the probability of non-extinction decays (exponentially)
 - ◆ The distribution of persistence times must be asymptotically exponential

Interpreting the quasi-equilibrium

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- The quasi-equilibrium is the asymptotic distribution of system states given that nothing has gone extinct
- The eigenvalue λ_q associated with the quasi-equilibrium distribution is the rate at which the probability of non-extinction decays (exponentially)
 - ◆ The distribution of persistence times must be asymptotically exponential
 - ◆ The expected persistence time (looking forward) approaches $-1/\lambda_q$ as the system continues to persist

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We model the ensemble distribution by creating one conceptual ‘box’ for each possible state of the system, and asking what is the probability that the system is in each box.

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We model the ensemble distribution by creating one conceptual ‘box’ for each possible state of the system, and asking what is the probability that the system is in each box.
 - ◆ This can be a lot of boxes

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We model the ensemble distribution by creating one conceptual ‘box’ for each possible state of the system, and asking what is the probability that the system is in each box.
 - ◆ This can be a lot of boxes
- The probabilities change as follows:

Modelling the ensemble distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We model the ensemble distribution by creating one conceptual ‘box’ for each possible state of the system, and asking what is the probability that the system is in each box.

- ◆ This can be a lot of boxes

- The probabilities change as follows:

- $$\dot{p}_S = \sum_{S'} p_{S'} r_{S' \rightarrow S} - p_S \sum_{S'} r_{S \rightarrow S'}$$

Modelling the quasi-distribution

- We can also model the probability of being in a particular state given that extinction has not occurred

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Modelling the quasi-distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient

Modelling the quasi-distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient
 - ◆ Can also keep track of cumulative extinction probability

Modelling the quasi-distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient
 - ◆ Can also keep track of cumulative extinction probability
- Define $q_S = p_S / (1 - p_N)$ where N is a ‘null’ state that we cannot escape from.

Modelling the quasi-distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient
 - ◆ Can also keep track of cumulative extinction probability
- Define $q_S = p_S / (1 - p_N)$ where N is a ‘null’ state that we cannot escape from.
- $$\dot{q}_S = \sum_{S'} q_{S'} r_{S' \rightarrow S} - q_S \sum_{S'} r_{S \rightarrow S'}$$

Modelling the quasi-distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient
 - ◆ Can also keep track of cumulative extinction probability
- Define $q_S = p_S / (1 - p_N)$ where N is a ‘null’ state that we cannot escape from.
- $\dot{q}_S = \sum_{S'} q_{S'} r_{S' \rightarrow S} - q_S \sum_{S'} r_{S \rightarrow S'}$
 - ◆ $-q_S r_{S \rightarrow N}$

Modelling the quasi-distribution

- Demographic stochasticity

- Introduction

- Describing a stochastic process

- Equilibrium and quasi-equilibrium

- Equilibrium
- Quasi-equilibrium

- Analytic methods

- Simulating distributions

- Simulating realizations

- Strain interactions

- Conclusions

- We can also model the probability of being in a particular state given that extinction has not occurred
 - ◆ Computationally convenient
 - ◆ Can also keep track of cumulative extinction probability
- Define $q_S = p_S / (1 - p_N)$ where N is a ‘null’ state that we cannot escape from.
- $\dot{q}_S = \sum_{S'} q_{S'} r_{S' \rightarrow S} - q_S \sum_{S'} r_{S \rightarrow S'}$
 - ◆ $-q_S r_{S \rightarrow N}$
 - ◆ $+q_S \sum_{S'} q_{S'} r_{S' \rightarrow N}$

The fate of infectious disease

■ Fizzle

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

The fate of infectious disease

- Fizzle
 - ◆ Disease fails to “establish”

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

■ Fizzle

- ◆ Disease fails to “establish”
- ◆ We will make this precise later

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Fizzle
 - ◆ Disease fails to “establish”
 - ◆ We will make this precise later
- Burn-out

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Fizzle
 - ◆ Disease fails to “establish”
 - ◆ We will make this precise later
- Burn-out
 - ◆ Disease goes extinct after first epidemic

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Fizzle
 - ◆ Disease fails to “establish”
 - ◆ We will make this precise later
- Burn-out
 - ◆ Disease goes extinct after first epidemic
- Fade-out

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Fizzle
 - ◆ Disease fails to “establish”
 - ◆ We will make this precise later
- Burn-out
 - ◆ Disease goes extinct after first epidemic
- Fade-out
 - ◆ Disease goes extinct after system approaches quasi-equilibrium

The fate of infectious disease

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

● Equilibrium

● Quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Fizzle
 - ◆ Disease fails to “establish”
 - ◆ We will make this precise later
- Burn-out
 - ◆ Disease goes extinct after first epidemic
- Fade-out
 - ◆ Disease goes extinct after system approaches quasi-equilibrium
 - ◆ Can take a *long* time

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Analytic methods

Linearization

- Two of the most useful tools for understanding deterministic disease models are linearization:

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● **Linearization**

● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Linearization

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● **Linearization**

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Two of the most useful tools for understanding deterministic disease models are linearization:
 - ◆ **Disease-free equilibrium:** what factors control whether the disease can invade and persist?

Linearization

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● **Linearization**

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Two of the most useful tools for understanding deterministic disease models are linearization:
 - ◆ **Disease-free equilibrium:** what factors control whether the disease can invade and persist?
 - ◆ **Endemic equilibrium:** tendency to cycle, damping or persistence of cycles

Linearization

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● **Linearization**

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Two of the most useful tools for understanding deterministic disease models are linearization:
 - ◆ **Disease-free equilibrium:** what factors control whether the disease can invade and persist?
 - ◆ **Endemic equilibrium:** tendency to cycle, damping or persistence of cycles
- Both of these methods have analogues in demographic models

Linear birth-death process

- We do an invasion analysis by asking how the number of infectives behaves in the limit where we assume that virtually the whole population is susceptible.

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● **Linear birth-death process**

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Linear birth-death process

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● **Linear birth-death process**

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We do an invasion analysis by asking how the number of infectives behaves in the limit where we assume that virtually the whole population is susceptible.
- This corresponds to a demographic model with the state determined by the number of infectious individuals I

Linear birth-death process

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We do an invasion analysis by asking how the number of infectives behaves in the limit where we assume that virtually the whole population is susceptible.
- This corresponds to a demographic model with the state determined by the number of infectious individuals I
- This system has only two events:

Linear birth-death process

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We do an invasion analysis by asking how the number of infectives behaves in the limit where we assume that virtually the whole population is susceptible.
- This corresponds to a demographic model with the state determined by the number of infectious individuals I
- This system has only two events:
 - ◆ Infection at rate $R_0 I$

Linear birth-death process

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We do an invasion analysis by asking how the number of infectives behaves in the limit where we assume that virtually the whole population is susceptible.
- This corresponds to a demographic model with the state determined by the number of infectious individuals I
- This system has only two events:
 - ◆ Infection at rate $R_0 I$
 - ◆ Recovery at rate I

Long-term behavior

- Unlike the finite systems discussed before, the probability of eventual extinction in this system is not one!

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Long-term behavior

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Unlike the finite systems discussed before, the probability of eventual extinction in this system is not one!
- Why not?

Long-term behavior

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Unlike the finite systems discussed before, the probability of eventual extinction in this system is not one!
- Why not?
 - ◆ Probability of extinction given persistence goes to zero, as expected number of infectious individuals goes to ∞

Extinction probability

- Chains of infection are independent in this model

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Extinction probability

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Chains of infection are independent in this model
- We can use this fact to solve directly for the probability of extinction when starting from I infections, E_I

Extinction probability

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Chains of infection are independent in this model
- We can use this fact to solve directly for the probability of extinction when starting from I infections, E_I
 - ◆ $E_I = R_0^{-I}$, when $R_0 > 1$

Extinction probability

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Extinction probability

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Chains of infection are independent in this model
- We can use this fact to solve directly for the probability of extinction when starting from I infections, E_I
 - ◆ $E_I = R_0^{-I}$, when $R_0 > 1$
 - ◆ 1, otherwise
- We can define this as the ‘fizzle’ probability: the disease would have gone extinct even without depleting any susceptibles.

Moment calculations

- Ask: what is the expected behavior of the mean, variance, ... of the ensemble?

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

■ Ask: what is the expected behavior of the mean, variance, ... of the ensemble?

■ Define: $\mu = \sum_I I p_i$

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- Ask: what is the expected behavior of the mean, variance, ... of the ensemble?
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- How does μ change through time?

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● **Moment calculations**

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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■ Define: $\mu = \sum_I I p_i$

■ How does μ change through time?

◆ $\dot{\mu} = \sum_I I \dot{p}_I$

◆ $= \sum_I (b_I - m_I) p_I$, where $b(I) = R_0 I$ is the ‘birth’ rate, and $m(I) = I$ is the ‘death’ rate

Moment calculations

- How does μ change through time in the linear system?

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process

● Extinction probability

● **Moment calculations**

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Moment calculations

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● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

■ How does μ change through time in the linear system?

◆ $\dot{\mu} = \sum_I (b_I - m_I)p_I$

■ The birth rate is $b(I) = R_0 I$

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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◆ $= (R_0 - 1) \mu$

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- How does μ change through time in the linear system?

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- The birth rate is $b(I) = R_0 I$

- The 'death' rate is $m(I) = I$

- ◆ $\dot{\mu} = \sum_I (R_0 I - I)p_I$

- ◆ $= (R_0 - 1) \sum_I I p_I$

- ◆ $= (R_0 - 1)\mu$

- The expected value (average over realizations) grows exponentially!

Moment calculations

- How does μ change through time in a non-linear system?

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- How does μ change through time in a non-linear system?

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$$\dot{\mu} = \sum_I (b_I - m_I) p_I$$

- ◆ In general, we expect each moment to depend on higher moments:

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - e.g., mean depends on variance and skewness

Moment calculations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization
● Linear birth-death process
● Extinction probability

● **Moment calculations**

● Moment-generating functions
● Invasion analysis
● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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- ◆ In general, we expect each moment to depend on higher moments:

- e.g., mean depends on variance and skewness

- Moment-closure techniques, and linearization approximations, can help.

Moment-generating functions

- We can use a very slick mathematical trick: define $\phi = \sum_I p_I x^I$.

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● **Moment-generating functions**

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Moment-generating functions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● **Moment-generating functions**

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We can use a very slick mathematical trick: define $\phi = \sum_I p_I x^I$.
- ◆ If we know the function $\phi(x)$ at a given time, we know all of the probabilities p_I .

Moment-generating functions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- **Moment-generating functions**
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Moment-generating functions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- **Moment-generating functions**
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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- For example, we can calculate the exact ensemble distribution through time of the linear birth-death process

Moment-generating functions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- **Moment-generating functions**
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ If we know the function $\phi(x)$ at a given time, we know all of the probabilities p_I .
- We can use our state/rate equations to write an expression for $\dot{\phi}$, which can be converted into a partial differential equation and analyzed, approximated, and (rarely) solved.
- For example, we can calculate the exact ensemble distribution through time of the linear birth-death process
 - ◆ Negative binomial with mean $I_0 \exp((R_0 - 1)t)$ and parameter I_0

Invasion analysis

Summary

- We understand exact behavior of linearized invasion model

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Invasion analysis

Summary

- We understand exact behavior of linearized invasion model
- This allows us to understand the properties of the SIR model, in the absence of effects due to depletion of susceptibles:

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Invasion analysis

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Summary

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Invasion analysis

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Fizzle probability
 - ◆ Size distribution of fizzled epidemics

Invasion analysis

Summary

- We understand exact behavior of linearized invasion model
- This allows us to understand the properties of the SIR model, in the absence of effects due to depletion of susceptibles:
 - ◆ Fizzle probability
 - ◆ Size distribution of fizzled epidemics
 - ◆ Mean and variance in epidemic growth rate

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

- We can approximate the discrete-valued demographic system with a real-valued system that reflects the mean *and variance* of the demographic system

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We can approximate the discrete-valued demographic system with a real-valued system that reflects the mean *and variance* of the demographic system
 - ◆ Thus we can incorporate demographic stochasticity in a continuous system

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Disease persistence

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Thus we can incorporate demographic stochasticity in a continuous system
 - ◆ An excellent approximation except when some values are very small
- In a linear (or linearized) system, we can solve the equilibrium distribution of the continuous equations, and thus approximate the quasi-equilibrium distribution
 - ◆ Disease persistence
 - ◆ Size of demographic fluctuations

Diffusion approximations

- We linearize about the endemic equilibrium, in exact analogy to Jacobian methods for stability in deterministic models

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations
● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We linearize about the endemic equilibrium, in exact analogy to Jacobian methods for stability in deterministic models
- Diffusion (and thus demographic stochasticity) is relatively unimportant when the square of the number infected is large compared to the demographic variance

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Number infected at equilibrium: $\frac{(R_0 - 1)\rho N}{R}$

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

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 - ◆ Number infected at equilibrium: $\frac{(R_0 - 1)\rho N}{R}$
 - $\approx \rho N$
 - ◆ Demographic variance: $\approx N$

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

- We linearize about the endemic equilibrium, in exact analogy to Jacobian methods for stability in deterministic models
- Diffusion (and thus demographic stochasticity) is relatively unimportant when the square of the number infected is large compared to the demographic variance
 - ◆ Number infected at equilibrium: $\frac{(R_0 - 1)\rho N}{R}$
 - $\approx \rho N$
 - ◆ Demographic variance: $\approx N$
- Diffusion index $\approx \rho^2 N$. If ρ is small, demographic stochasticity can be important even for very large populations.

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

● Linearization

● Linear birth-death process

● Extinction probability

● Moment calculations

● Moment-generating functions

● Invasion analysis

● Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations
- Not a good estimate of extinction threshold

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations
- Not a good estimate of extinction threshold
 - ◆ Extinction is a global problem

Diffusion approximations

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations
- Not a good estimate of extinction threshold
 - ◆ Extinction is a global problem
 - ◆ Small diffusion index implies no extinction

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations
- Not a good estimate of extinction threshold
 - ◆ Extinction is a global problem
 - ◆ Small diffusion index implies no extinction
 - ◆ Large diffusion index implies non-local behavior

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

Diffusion approximations

Summary

- Linearization tells us *local* behavior of system
- Diffusion approximation is approximate
- Good estimate of the size of small oscillations
- Not a good estimate of extinction threshold
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 - ◆ Large diffusion index implies non-local behavior
- Reference: Nasell 1999 (on ASI site)

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

- Linearization
- Linear birth-death process
- Extinction probability
- Moment calculations
- Moment-generating functions
- Invasion analysis
- Diffusion approximations

Simulating distributions

Simulating realizations

Strain interactions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

● Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Simulating distributions

Simulating distributions

- Practical for medium-sized “one-dimensional” systems or small “two-dimensional” systems

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

● Simulating distributions

Simulating realizations

Strain interactions

Conclusions

Simulating distributions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

● Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Practical for medium-sized “one-dimensional” systems or small “two-dimensional” systems
- Write differential equations and simulate

Simulating distributions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

● Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Practical for medium-sized “one-dimensional” systems or small “two-dimensional” systems
- Write differential equations and simulate
- The “quasi-” equations may work better, numerically

Simulating distributions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

● Simulating distributions

Simulating realizations

Strain interactions

Conclusions

- Practical for medium-sized “one-dimensional” systems or small “two-dimensional” systems
- Write differential equations and simulate
- The “quasi-” equations may work better, numerically
- There are probably tricks for finding approximate answers without modelling the whole state space

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

- Lagrangian and Eulerian views
- Markovian
- Queueing
- Dynamic updating

Strain interactions

Conclusions

Simulating realizations

Lagrangian and Eulerian views

■ In fluid mechanics:

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?
 - ◆ Lagrangian refers to fluid-based viewpoint

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?
 - ◆ Lagrangian refers to fluid-based viewpoint
 - Analogous models of disease which follow each individual

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?
 - ◆ Lagrangian refers to fluid-based viewpoint
 - Analogous models of disease which follow each individual
- Does individual-based mean:

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?
 - ◆ Lagrangian refers to fluid-based viewpoint
 - Analogous models of disease which follow each individual
- Does individual-based mean:
 - ◆ Demographic?

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- In fluid mechanics:
 - ◆ Eulerian means a streambed-based viewpoint
 - Analogous to ‘box’ models of disease: how many people are here?
 - ◆ Lagrangian refers to fluid-based viewpoint
 - Analogous models of disease which follow each individual
- Does individual-based mean:
 - ◆ Demographic?
 - ◆ Lagrangian?

Lagrangian and Eulerian views

■ Box view (Eulerian)

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)
 - ◆ Allows for realistic detail

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)
 - ◆ Allows for realistic detail
 - Time distributions

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)
 - ◆ Allows for realistic detail
 - Time distributions
 - Infection history

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)
 - ◆ Allows for realistic detail
 - Time distributions
 - Infection history
- Combined view

Lagrangian and Eulerian views

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Box view (Eulerian)
 - ◆ Usually more convenient
 - Fast simulation
 - Analytic techniques
- Individual view (Lagrangian)
 - ◆ Allows for realistic detail
 - Time distributions
 - Infection history
- Combined view
 - ◆ We can also use simple Eulerian models to *approximate* more realistic Lagrangian simulations

Exponential distributions

- The Markovian assumption is equivalent to assuming exponential time distributions of events

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Exponential distributions

- The Markovian assumption is equivalent to assuming exponential time distributions of events
 - ◆ Can be spectacularly unrealistic

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Exponential distributions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- The Markovian assumption is equivalent to assuming exponential time distributions of events
 - ◆ Can be spectacularly unrealistic
 - Does this mean that classical models are stupid?

Exponential distributions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- The Markovian assumption is equivalent to assuming exponential time distributions of events
 - ◆ Can be spectacularly unrealistic
 - Does this mean that classical models are stupid?
 - The assumption needs to be evaluated in terms of the question the model is asking: how much does the assumption effect the dynamics?

An exponential distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

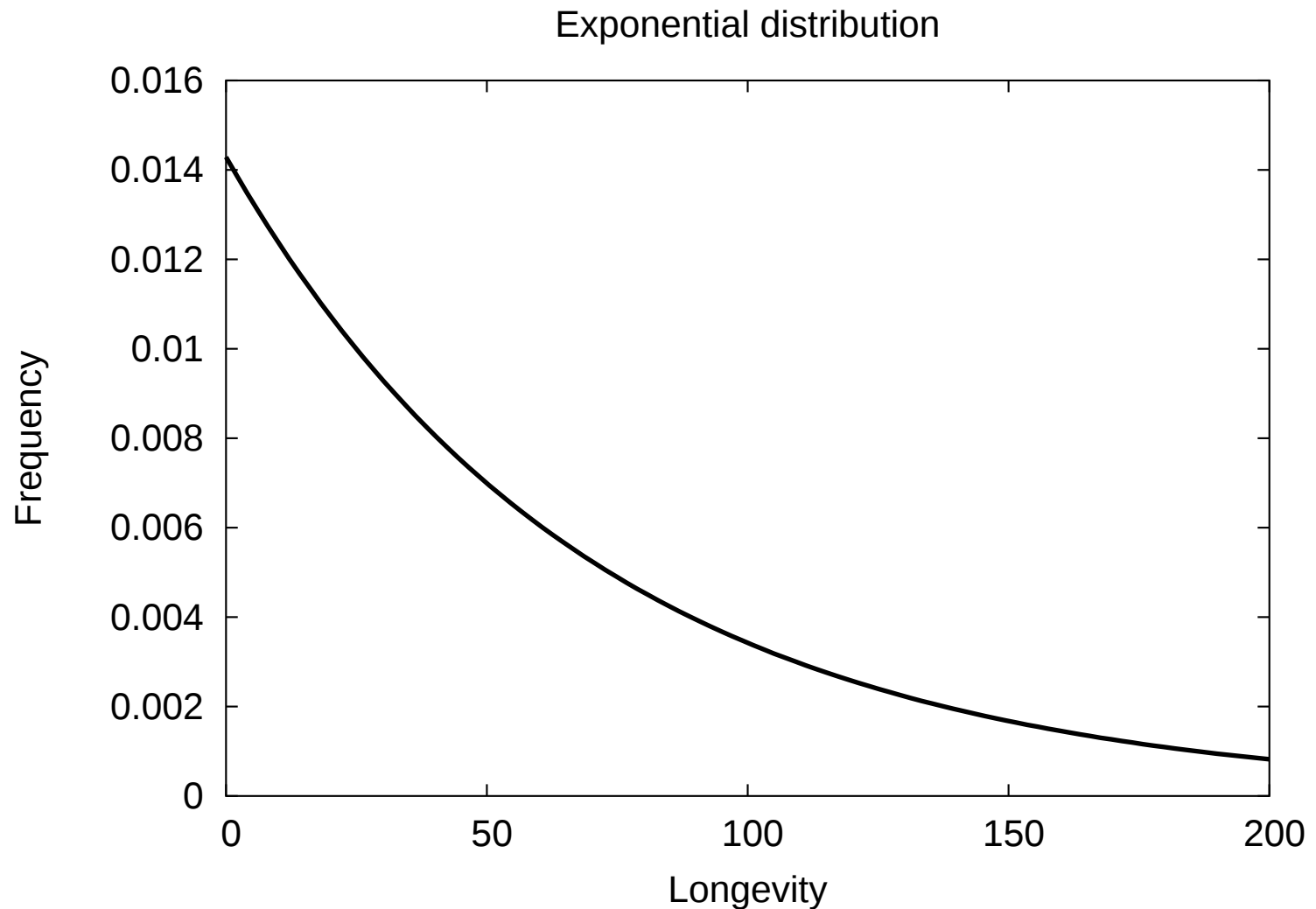
● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions



A normal distribution

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

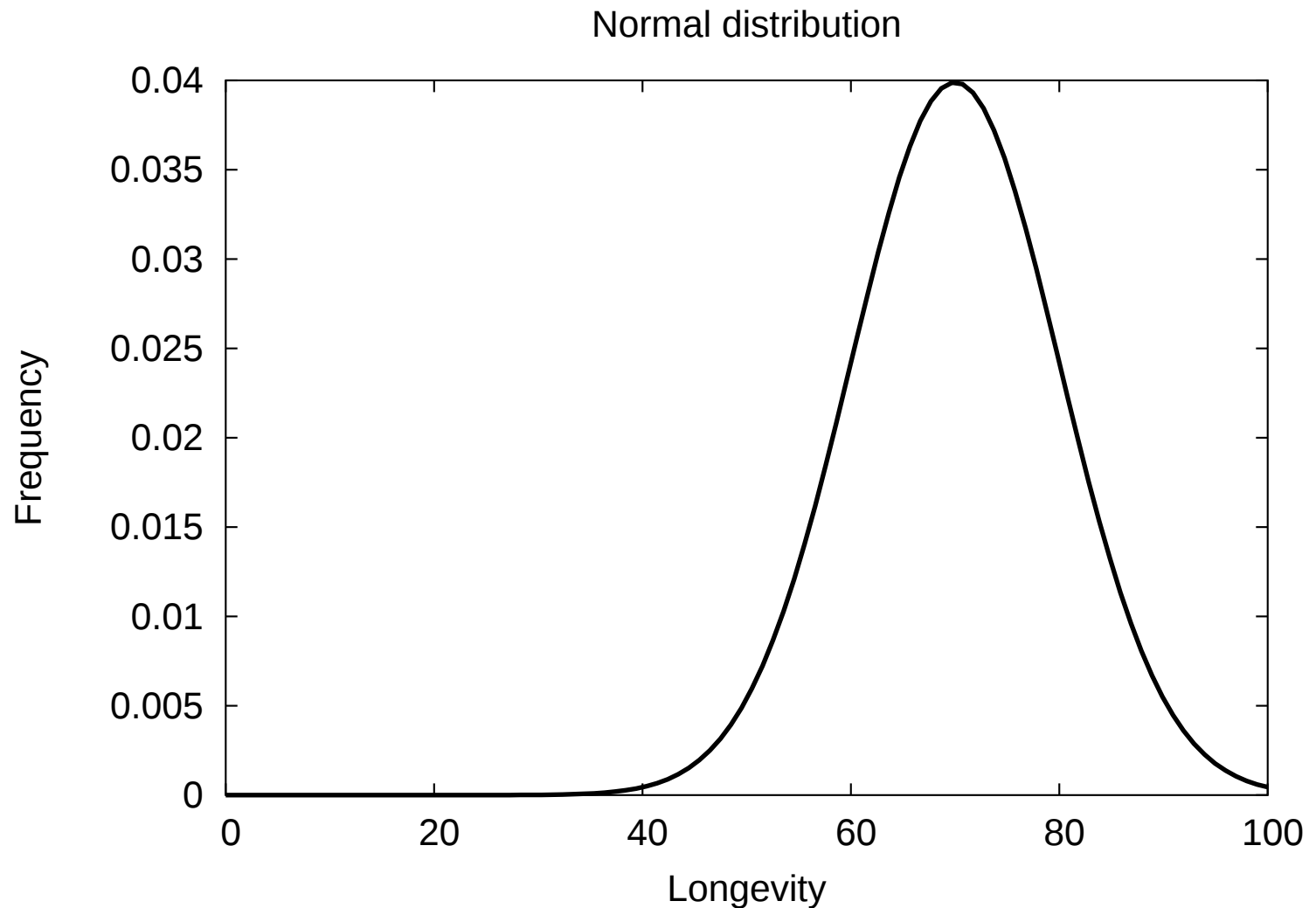
● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions



Practical simulation modelling

■ Eulerian (Markovian) approach

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Practical simulation modelling

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Eulerian (Markovian) approach
 - ◆ Erlang and pseudo-Erlang distributions

Practical simulation modelling

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Eulerian (Markovian) approach
 - ◆ Erlang and pseudo-Erlang distributions
- Lagrangian extensions

Practical simulation modelling

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Eulerian (Markovian) approach
 - ◆ Erlang and pseudo-Erlang distributions
- Lagrangian extensions
 - ◆ Queueing

Practical simulation modelling

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Eulerian (Markovian) approach
 - ◆ Erlang and pseudo-Erlang distributions
- Lagrangian extensions
 - ◆ Queueing
 - ◆ Dynamic updating

Markovian

■ Given a state of the system:

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Markovian

- Given a state of the system:
 - ◆ List possible events, and associated rates

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$
 - ◆ The probability of event E is r_E/r_T

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$
 - ◆ The probability of event E is r_E/r_T
 - ◆ Randomly select the time and nature of the next event

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$
 - ◆ The probability of event E is r_E/r_T
 - ◆ Randomly select the time and nature of the next event
 - ◆ Change the system state appropriately

Markovian

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● **Markovian**

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- Given a state of the system:
 - ◆ List possible events, and associated rates
 - ◆ Calculate the total rate r_T : this gives the rate at which the next event (whatever it is) will happen
 - i.e., an exponential waiting time with mean $1/r_T$
 - ◆ The probability of event E is r_E/r_T
 - ◆ Randomly select the time and nature of the next event
 - ◆ Change the system state appropriately
 - ◆ Repeat forever

Queueing

- One practical way to extend a model to allow non-Markovian (and non-Eulerian) complications is to keep of ‘queue’ of events that are slated to happen

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

- Lagrangian and Eulerian views
- Markovian
- Queueing
- Dynamic updating

Strain interactions

Conclusions

Queueing

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- One practical way to extend a model to allow non-Markovian (and non-Eulerian) complications is to keep of ‘queue’ of events that are slated to happen
 - ◆ Queue is sorted chronologically

Queueing

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

- Lagrangian and Eulerian views
- Markovian
- Queueing
- Dynamic updating

Strain interactions

Conclusions

- One practical way to extend a model to allow non-Markovian (and non-Eulerian) complications is to keep of ‘queue’ of events that are slated to happen
 - ◆ Queue is sorted chronologically
 - ◆ At each step perform the next event, and add events triggered by it to the queue

Queueing

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

- Lagrangian and Eulerian views
- Markovian
- Queueing
- Dynamic updating

Strain interactions

Conclusions

- One practical way to extend a model to allow non-Markovian (and non-Eulerian) complications is to keep of ‘queue’ of events that are slated to happen
 - ◆ Queue is sorted chronologically
 - ◆ At each step perform the next event, and add events triggered by it to the queue
 - When somebody is born, add their death to the queue

Queueing

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- One practical way to extend a model to allow non-Markovian (and non-Eulerian) complications is to keep of ‘queue’ of events that are slated to happen
 - ◆ Queue is sorted chronologically
 - ◆ At each step perform the next event, and add events triggered by it to the queue
 - When somebody is born, add their death to the queue
 - When somebody is infected, add their recovery, potentially infectious contacts to the queue

Dynamic updating

- If we assume that potentially infectious contacts are Markovian, we can model efficiently using dynamic updating:

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

Dynamic updating

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- If we assume that potentially infectious contacts are Markovian, we can model efficiently using dynamic updating:
 - ◆ Choose a potential infector at random and update their state

Dynamic updating

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

● Lagrangian and Eulerian views

● Markovian

● Queueing

● Dynamic updating

Strain interactions

Conclusions

- If we assume that potentially infectious contacts are Markovian, we can model efficiently using dynamic updating:
 - ◆ Choose a potential infector at random and update their state
 - ◆ If the infector is infectious, choose a potential infectee at random and update their state

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

● Markov (exponential) waiting times

● Realistic (Gaussian) waiting times

Conclusions

Strain interactions

Multiple strains

- Many pathogens have different competing strains, and often new ones evolve on relatively short time scales

- Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

- Markov (exponential) waiting times

- Realistic (Gaussian) waiting times

Conclusions

Multiple strains

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

● Markov (exponential) waiting times

● Realistic (Gaussian) waiting times

Conclusions

- Many pathogens have different competing strains, and often new ones evolve on relatively short time scales
- This is another area where including demographic stochasticity has important effects

Markov (exponential) waiting times

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

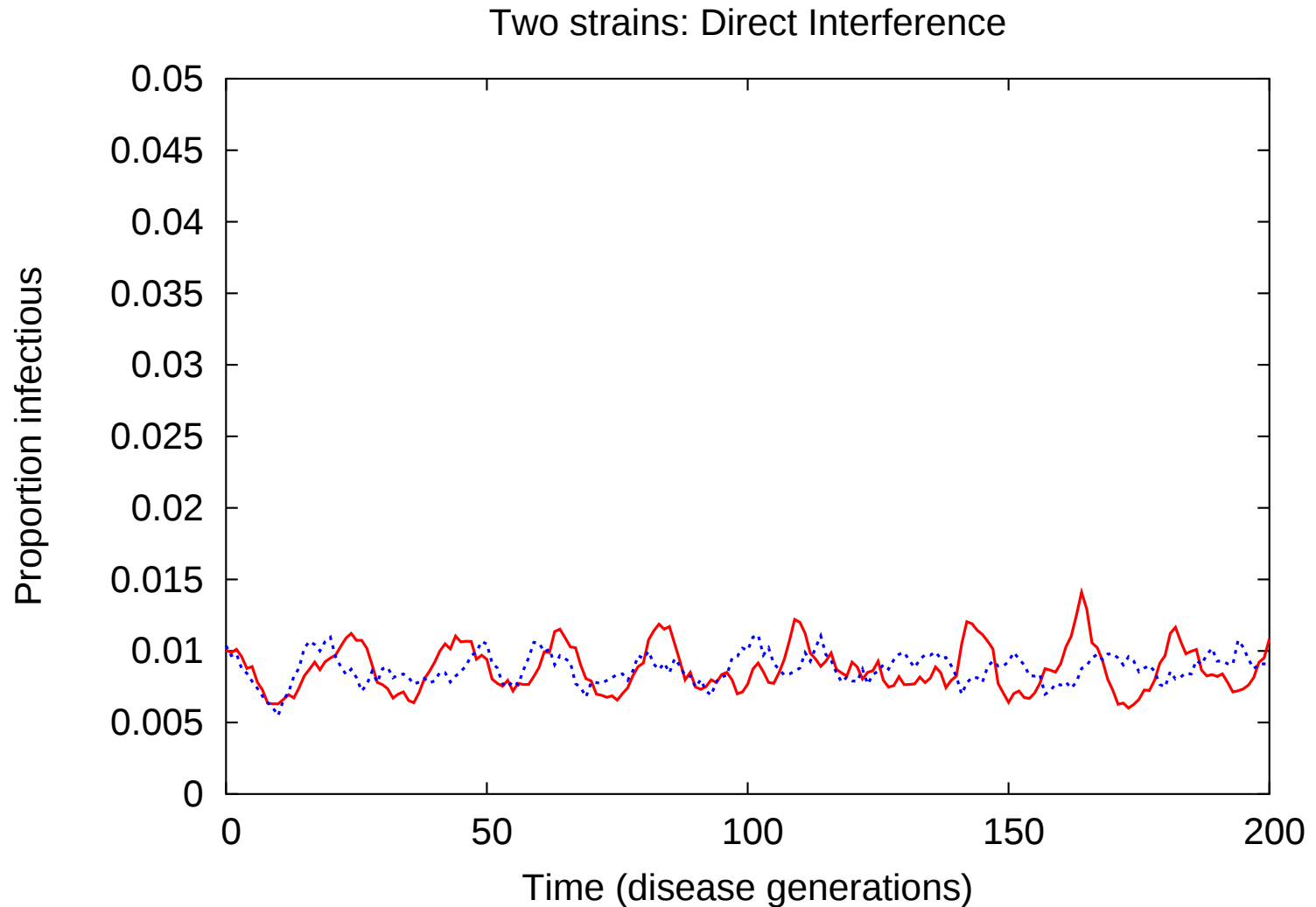
Simulating realizations

Strain interactions

● Markov (exponential) waiting times

● Realistic (Gaussian) waiting times

Conclusions



Realistic (Gaussian) waiting times

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

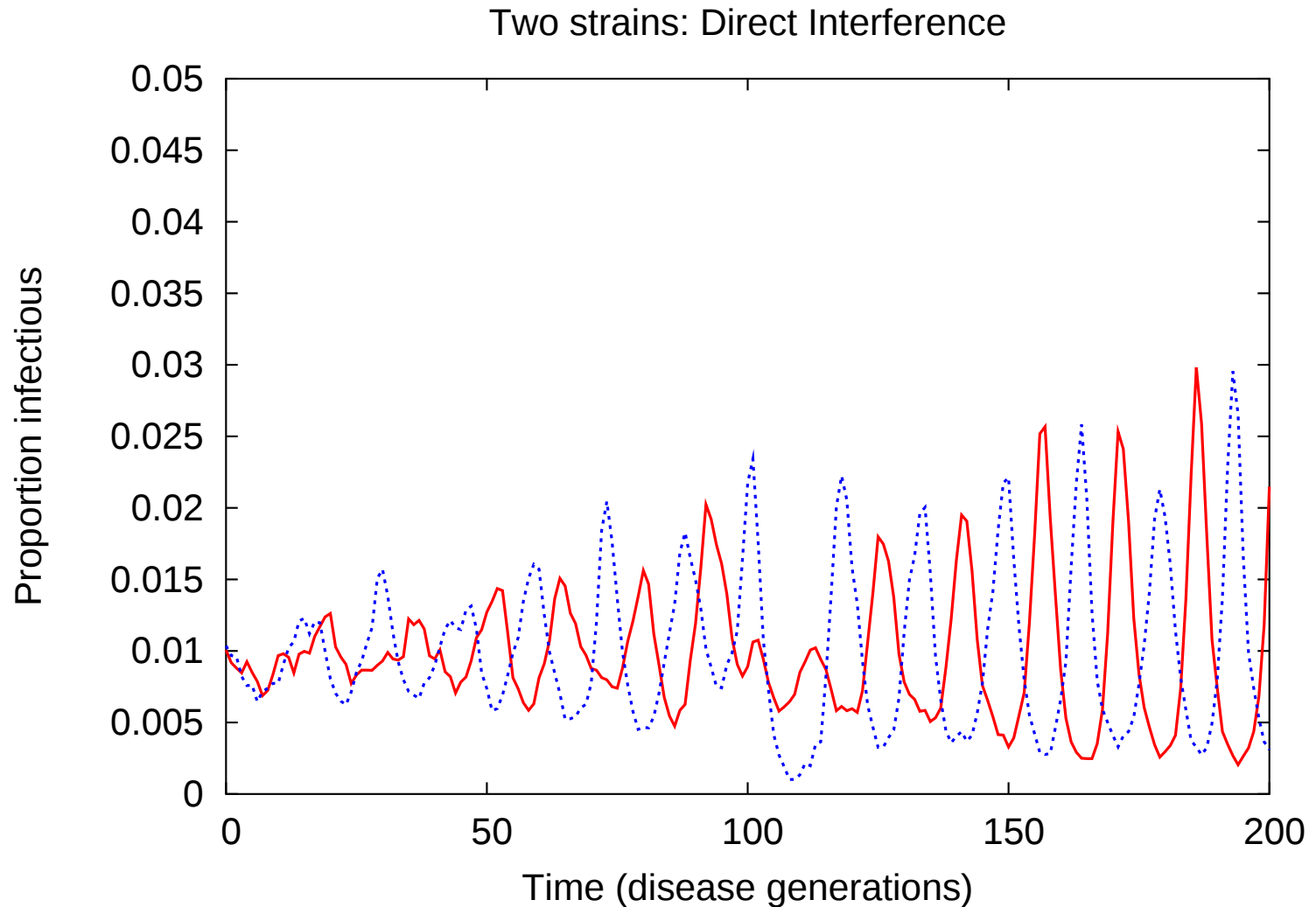
Simulating realizations

Strain interactions

● Markov (exponential) waiting times

● Realistic (Gaussian) waiting times

Conclusions



● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

Conclusions

Conclusions

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● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

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Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

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Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

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Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

● Conclusions

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 - ◆ Simulating realizations

Conclusions

● Demographic stochasticity

Introduction

Describing a stochastic process

Equilibrium and quasi-equilibrium

Analytic methods

Simulating distributions

Simulating realizations

Strain interactions

Conclusions

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- Remember: demographic stochasticity is real!