

Analysing Change One Step at a Time

CMEE Maths Week

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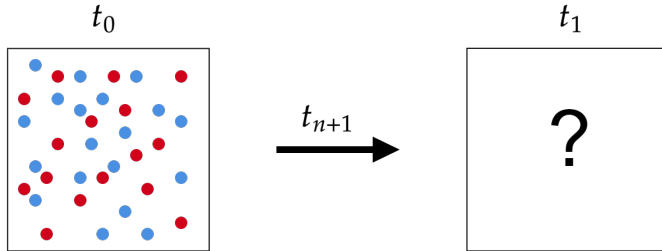
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Example: Haploid Genetics

1 Discrete Models

Consider a population of haploid organisms and a locus with alleles A and a . How can we analyse the distribution of alleles in this population through time?



Haploid Genetics: Setup

1 Discrete Models

Before we can do anything, we need some information.

- The total number of individuals in the first generation - N_0 .
- The initial number of each allele in the population - N_0^A and N_0^a .
- The fitness coefficient conferred by each allele - r_A and r_a .

Here we define fitness as the contributions in offspring that each allele has to the next generation.

Haploid Genetics: Equations

1 Discrete Models

Now we can propose a model of how the next generation will look like:

- Evolution of individuals with allele A - $N_{n+1}^A = r_A N_n^A$
- Evolution of individuals with allele a - $N_{n+1}^a = r_a N_n^a$
- Evolution of the population size - $N_{n+1} = r_A N_n^A + r_a N_n^a$

With this simple model, we can predict the distribution of alleles within the population for a given number of generations.

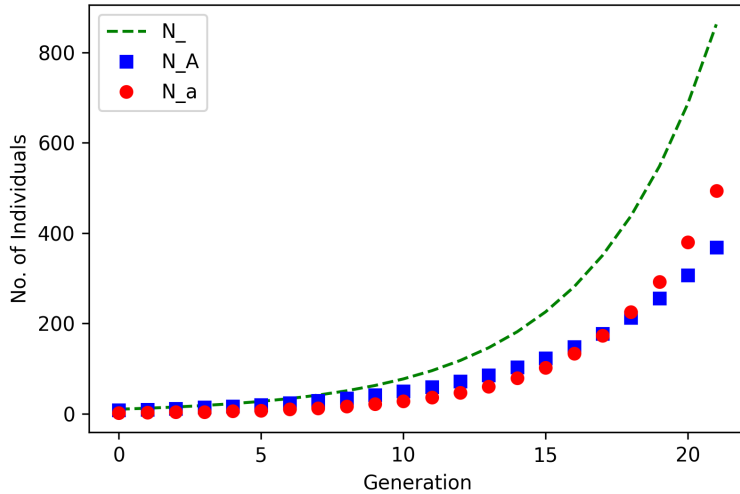


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Sequences

2 Sequences

This last example makes use of a key concept: **sequences**. Formally, we define a sequence as a function $f : \mathbb{N} \rightarrow \mathbb{R}$, that is, every natural number gets mapped to a real value. Sequences come in two basic flavours:

- **Recursive sequences** - $f(n)$ depends on previous values of the sequence.
- **Explicit sequences** - $f(n)$ depends only on n .

Some recursive sequences have explicit forms, but most do not.

Haploid Genetics: Making it Explicit

2 Sequences

The model we proposed to describe haploid allele distributions has an issue: you have to compute every previous generation to get to the one you want. Fortunately, we can fix this.

$$N_{n+1}^A = r_A N_n^A = r_A^2 N_{n-1}^A = \cdots = r_A^{n+1} N_0^A$$

$$N_{n+1}^a = r_a N_n^a = r_a^2 N_{n-1}^a = \cdots = r_a^{n+1} N_0^a$$

$$N_{n+1} = r_A^{n+1} N_0^A + r_a^{n+1} N_0^a$$

Now we only need to know what the initial population looks like!

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Haploid Genetics: Divergence

3 Sequence Limits

As we change our model's description to an explicit expression, we notice an important flaw, for large enough fitness coefficients, $r > 1$, the population grows unbounded.

$$\lim_{n \rightarrow \infty} N_{n+1} = \lim_{n \rightarrow \infty} r_A^{n+1} N_0^A + r_a^{n+1} N_0^a \rightarrow \infty$$

In this case we say that the underlying sequence is **divergent**, it blows up with continued iteration.

Divergent Sequences

3 Sequence Limits

Making use of our last example, we can give a concrete definition of divergent sequences. We say a sequence $\{a_n\}$ is divergent if:

$$\lim_{n \rightarrow \infty} a_n \rightarrow \pm\infty$$

This is not the same as saying that the limit is $\pm\infty$, instead it implies that $\{a_n\}$ approaches infinity but the limit does not exist.

Haploid Genetics: Allele Frequencies

3 Sequence Limits

Before we leave this example, let's look at a more informative measure of allele distributions, their frequencies:

- Frequency of allele A in the n^{th} generation - $F_n^A = \frac{N_n^A}{N_n} = \frac{r_A^n N_0^A}{r_A^n N_0^A + r_a^n N_0^a}$
- Frequency of allele a in the n^{th} generation - $F_n^a = \frac{N_n^a}{N_n} = \frac{r_a^n N_0^a}{r_A^n N_0^A + r_a^n N_0^a}$

Now let's try and get an idea of what their **long-term behaviour** will look like.

Haploid Genetics: Convergence

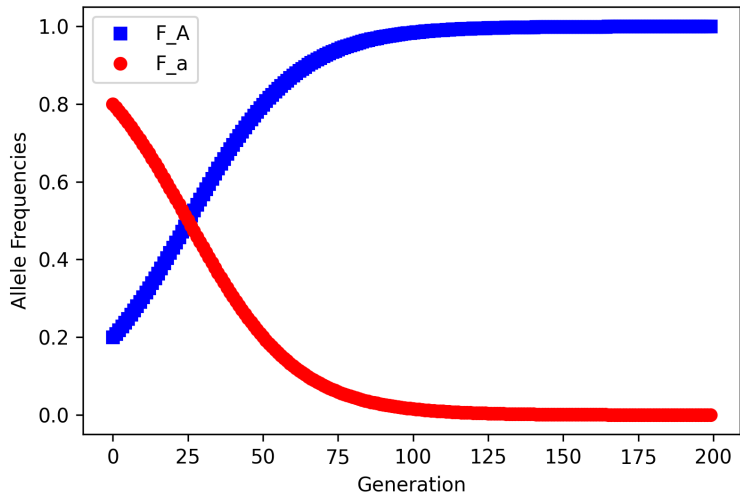
3 Sequence Limits

With a little algebra we can rewrite our equations for allele frequencies:

$$F_n^A = \frac{\left(\frac{r_A}{r_a}\right)^n N_0^A}{\left(\frac{r_A}{r_a}\right)^n N_0^A + N_0^a} \quad F_n^a = \frac{\left(\frac{r_a}{r_A}\right)^n N_0^a}{\left(\frac{r_a}{r_A}\right)^n N_0^a + N_0^A}$$

Let's assume, that $r_A > r_a$. With a little work, we can show that, as time goes on, both of these sequences approach a finite number. In other words, the sequences **converge** to a **limit** L .

$$\lim_{n \rightarrow \infty} F_n^A = L_A \quad \lim_{n \rightarrow \infty} F_n^a = L_a$$



Convergent Sequences

3 Sequence Limits

So generalizing the last example, we say a sequence $\{a_n\}$ converges if there exists an L , such that:

$$\lim_{n \rightarrow \infty} a_n = L$$

Furthermore L is known as the limit of $\{a_n\}$.

Properties of Limits

3 Sequence Limits

Let us take this opportunity to list some of the properties of limits. Consider two convergent sequences $\{a_n\}$ and $\{b_n\}$, such that $\lim a_n = L$ and $\lim b_n = M$, it can be proven that the following properties are true:

- $\lim(a_n + b_n) = \lim a_n + \lim b_n = L + M$
- $\lim(Ca_n) = C \lim a_n = CL$, for any $C \in \mathbb{R}$
- $\lim(a_n b_n) = \lim(a_n) \lim(b_n) = LM$
- $\lim \frac{a_n}{b_n} = \frac{\lim a_n}{\lim b_n} = \frac{L}{M}$, so long as $M \neq 0$

These properties facilitate the calculation of limits for sequences composed of two or more simpler sequences.

Non-Convergent Sequences

3 Sequence Limits

We've seen that sequences can either converge to a finite limit or diverge to infinity, however, there is a third possibility: **non-convergence**.

- **Periodicity and Limit Cycles:** for large enough n , there exists $T \in \mathbb{N}$ such that $f(n) = f(n + T)$.
- **Deterministic Chaos:** long term behaviour is seemingly random and sensitive to initial conditions.

To illustrate non-convergent sequences and introduce some useful tools, let's look at another example.

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Example: The Logistic Map

4 Fixed Points and Stability

Let's imagine a population of size N_0 , we propose a model where, at low density, the population grows at rate r , and as the population approaches a **carrying capacity** K the growth rate decreases proportionally to population density.

$$N_{n+1} = N_n r \left(1 - \frac{N_n}{K} \right)$$

This is an example of a **density dependent** population model, known as the **Logistic** difference equation, and despite its simplicity, it can exhibit richly complex behaviours.

The Logistic Map: Canonical Form

4 Fixed Points and Stability

To make things simpler we introduce a change of variable $X_n = \frac{N_n}{K}$, and rewrite the logistic equation in terms of X_n :

$$X_{n+1} = X_n r (1 - X_n)$$

Note that to avoid trivial extinctions, we need to constrain X_0 : $0 < X_0 < 1$, which essentially means that the population cannot exceed its carrying capacity.

The Logistic Map: Fixed Points

4 Fixed Points and Stability

One way of inferring a difference equation's long term behaviour is to find its **fixed points**. To do this, we assume the existence of a fixed point X^* such that:

$$X^* = X^*r(1 - X^*) \Rightarrow r(X^*)^2 + (1 - r)X^* = 0$$

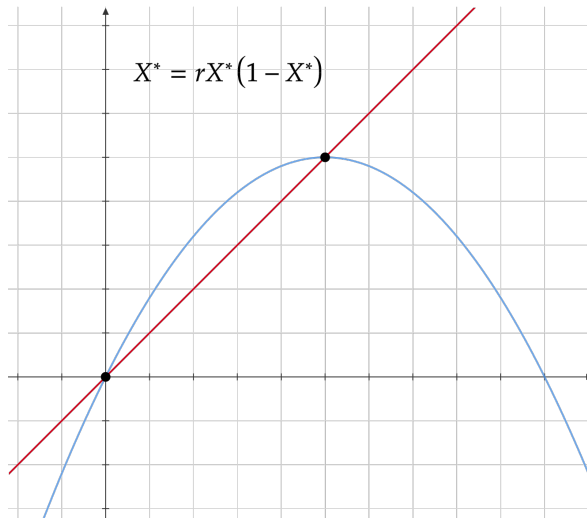
Solving this quadratic equation gives us the fixed points:

$$X^* = 0 \quad \text{and} \quad X^* = 1 - \frac{1}{r}$$

Fixed points tell you where the sequence will stop changing with subsequent iterations, however, they are only candidates for long term behaviour.

Geometric View of Fixed Points

4 Fixed Points and Stability



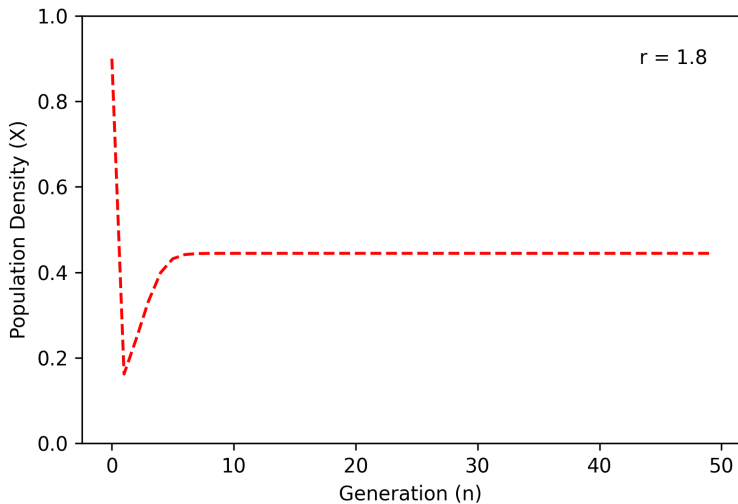
The Logistic Map: Stable Attractors

4 Fixed Points and Stability

The logistic map's behaviour is almost entirely determined by the intrinsic growth rate r . For example, for $1 < r \leq 2$, X_n will quickly approach $X^* = 1 - \frac{1}{r}$.

- X^* is known as a **stable attractor** of the system.
- X_n will converge to X^* so long as $X_0 > 0$.

Stable Attractor



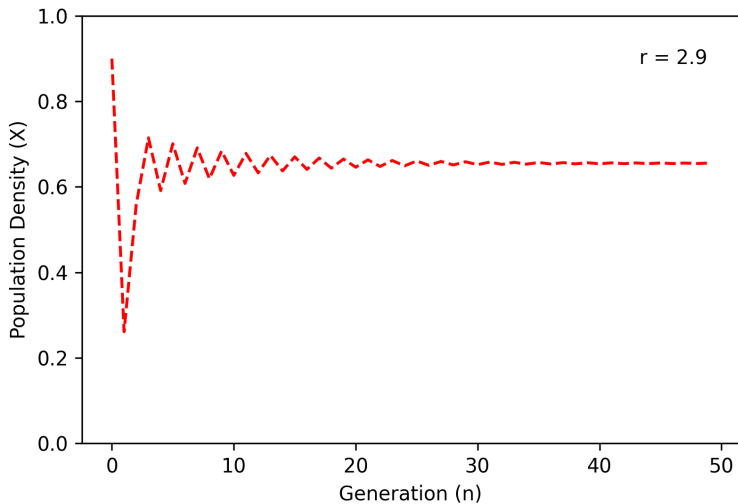
The Logistic Map: Approaching Critical Stability

4 Fixed Points and Stability

For $2 < r \leq 3$ the logistic map approaches $X^* = 1 - \frac{1}{r}$ more slowly, fluctuating around X^* before settling.

- As $r \rightarrow 3$, X_n will take longer to reach X^* .
- For $r = 3$ we are at the threshold between a stable fixed point and **critical stability**.

Fluctuations around X^*



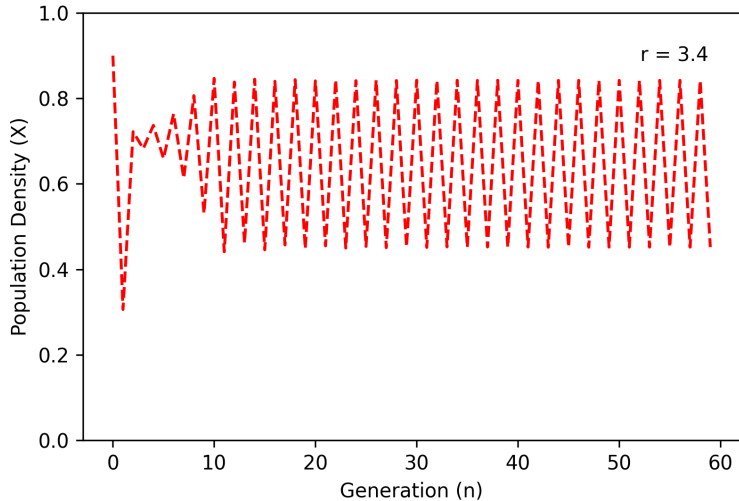
Critical/Marginal Stability

4 Fixed Points and Stability

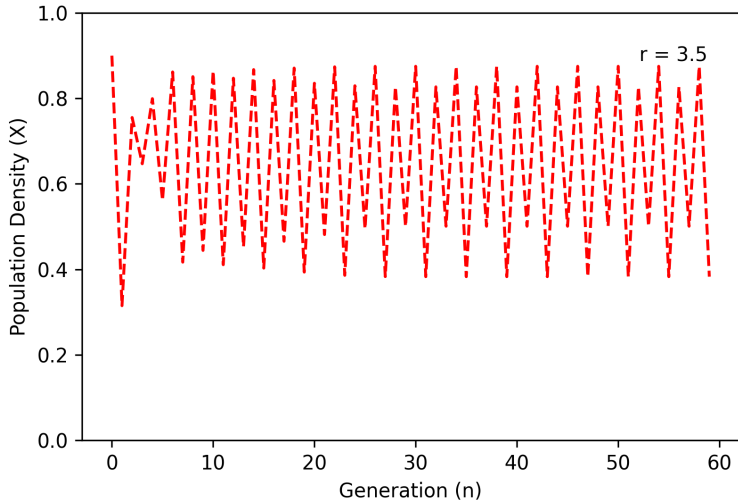
When $3 < r < 3.56995$, X_n no longer approaches a stable fixed point, but settles in to periodic fluctuations called **limit cycles**.

- Limit cycles are periodic fluctuations around a defined set of points.
- As r increases from $3 \rightarrow 3.56995$, X_n 's limit cycles become more complex, first oscillating between 2 points, then 4, 8, 16, etc. This is known as a **Period Doubling Cascade**.

Two Limit Cycle



Four Limit Cycle



The Logistic Map: Chaos

4 Fixed Points and Stability

Increasing r beyond $r = 3.56995$ (approximately) will almost always exhibit **chaotic** behaviour. Chaos in dynamical systems is difficult to characterise due to its complexity.

- Chaotic systems are extremely sensitive to initial conditions.
- X_n does not settle into any predictable long term pattern.

Chaos

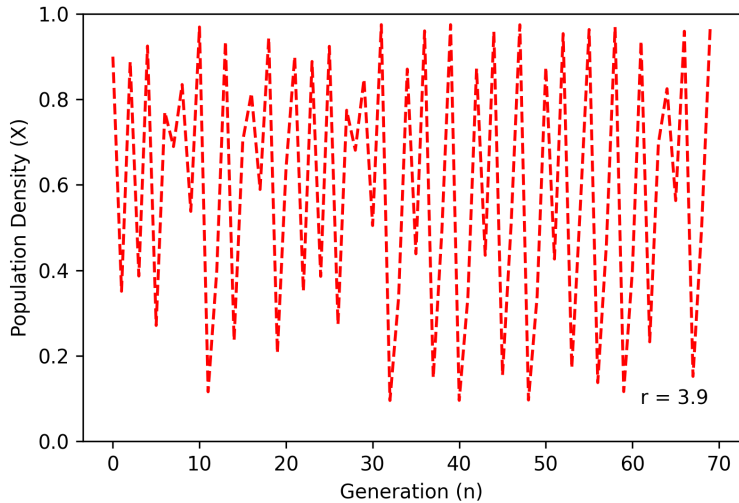


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When to be Discrete

5 Discrete Time Models Use Case

As we'll see later on, it is possible to define similar models using a different paradigm with continuous functions. Thus the question arises, when are discrete time models preferable?

- Population breeds at discrete time intervals.
- Organisms in population develop through discrete life-history stages.
- One or more limiting resources have discrete behaviour.
- etcetera . . .

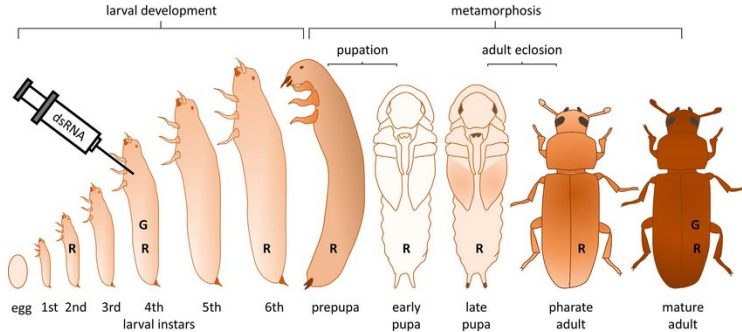
Synchronized Breeding

5 Discrete Time Models Use Case



Life-History Stages

5 Discrete Time Models Use Case



T. Walski *et al.*, 2016, Nature, Scientific Reports