Projects

The goals of these projects are to:

- apply some of the methods covered in the course;
- see what a (very short) theory project looks like;
- practise communicating modelling results;
- tackle a biologically relevant question in evolutionary biology.

You may use mathematical analysis, individual-based simulations, or ideally both. Groups were formed to combine complementary skills, make use of this diversity !

The outcome is a **10–15 minute group presentation** in two days, followed by 5 minutes of questions. This is ambitious, but we'll guide you along the way. Each assistant supervises two groups so ask them lots of questions or they'll be bored! And don't forget what you learnt with Thomas and Vitor re:presentations.

Group assignments

Group 1	Group 2	Group 3
Maya Louage	Ritam Das	George Shillcock
Raquel N. Palmeira	Lewis Flintham	Diane Douet
Aryan Golzaryan	Amanda B. Campos	Chon I Kam
Ayush Valecha	Dhanya Bharath	Ekaterine Kikodze

Group 4	Group 5	Group 6
João Valeriano	Isabel Rathmann	Tristan Canterbury
Izabel Salvi	Asad Hasan	Mathilda Whittle
Clemens Hacke	Julie Roux	Daniel Sankey
Julia N. Acquaviva	Rahul Jaitly	Niccole Porras
		Kingsley Hunt

Projects

Project 1: Do reciprocity and kin selection interact?

Project 2: When does predation favour prey diversification?

Project 3: How easily does mutualism evolve?

Project 4: What can drive the evolution of accelerated senescence?

Project 5: What drives the evolution of dispersal?

Project 6: When does temporal heterogeneity favour polymorphism?

For each project, I provide a short motivation and a suggested framework (life cycle + evolving traits). You are encouraged to look at the literature for context. These are classical questions in evolutionary ecology that have already been studied. The aim is not to make new discoveries, but to practise tackling such questions with the tools we learned, and to teach each other things we may not all know.

Project 1: Do reciprocity and kin selection interact?

Reciprocity and kin selection are two mechanisms that favour the evolution of helping behaviours. But can these interact? In other words: how does reciprocity evolve in a group-structured population under limited dispersal?

Proposed framework: Consider a subdivided population with the following life cycle :

1. Adults interact in pairs within groups and each chooses an action $a_\bullet = a(z_\bullet, z_1)$ (investment into cooperation) depending on its trait $z_\bullet$ and that of its partner z_1.
2. Each individual obtains a payoff $\pi(a_\bullet, a_1) = 1 + b\,a_1 - c\,a_\bullet$, determined by its own investment and that of its partner. Payoff maps to fecundity.
3. Adults produce offspring in proportion to their fecundity.
4. Offspring disperse with probability m or remain philopatric.
5. One randomly chosen adult per group dies and offspring compete locally for the vacant spot.

If possible, add an explicit behavioural layer where actions are the equilibrium outcome of a dynamical response process, e.g. :

$$\begin{aligned} \frac{da_{\bullet,t}}{dt} &= a_0 - a_{\bullet,t} + z_{\bullet}\, a_{1,t}, \\ \frac{da_{1,t}}{dt} &= a_0 - a_{1,t} + z_1\, a_{\bullet,t}. \end{aligned} \tag{1}$$

Here the evolving trait z controls responsiveness to a partner's previous investment, corresponding to reciprocity. At equilibrium $(t \to \infty)$, $a_{\bullet} = a_{\bullet,t}$ and $a_1 = a_{1,t}$.

Questions that can be explored:

- Does limited dispersal amplify or weaken the scope for the evolution of reciprocity?
- How do kin selection and reciprocity combine?

Project 2: When does predation favour prey diversification?

Predators often develop *search images* for common prey types through learning. This increases predation on common phenotypes and relaxes it on rare ones, generating negative frequency-dependent selection that can promote diversification.

Proposed framework: Consider a semelparous well-mixed homogeneous prey population of size N_t at generation t with the following life cycle:

1. Each adult produces a Poisson distributed number of offspring and then die. An individual with trait z produces on average $r_0(z)\exp(-\gamma N_t)$ offspring, where $\gamma > 0$ controls the strength of density dependent competition for reproductive resources and $r_0(z) = f_{\max}\exp(-z^2/\sigma^2)$ is the greatest average fecundity of an individual with trait z (maximised for $z = 0$ and with selection strength controlled by σ).

2. Predators form a **search image** from the current trait distribution in the prey. One model for this assumes the predator's attention field for trait z is given by

   $$L(z) \;=\; \frac{1}{B}\sum_{j=1}^{B} K_\tau(z - z_j), \qquad \text{where } K_\tau(u) = \exp\Big(-\frac{u^2}{\tau^2}\Big),$$

   where B is the number of offspring, z_j is the trait offspring indexed j, and $\tau > 0$ is parameter that determines how focused the predator's attention is on common phenotypes. When $L(z)$ is large, predators have learnt to associate z with prey and will therefore focus their attention on individuals that express z.
3. Survival from predation for an offprinting with trait z then is is

   $$s(z) = \frac{1}{1 + \alpha L(z)},$$

   where $\alpha > 0$ measures how strongly predators focus on common types.
4. Offspring that survive predation become the adults at $t{+}1$.

Questions that can be explored

- Under which conditions does predator learning make prey types diversify?
- How does predation-driven diversification affect overall population size and stability?
- Does predation-driven diversification lead to the stable coexistence of prey morphs, or to cycles of rise and fall in different types?
- How do ecological factors (competition for resources, crowding) interact with predator learning to shape prey diversity?

Project 3: How easily does mutualism evolve?

Reciprocity can evolve within species, but many reciprocal exchanges occur between species (e.g. arbuscular mycorrhizal fungi–plants, plant–pollinator systems). How do such mutualisms evolve and how stable are they?

Proposed framework: Consider two species A and B coexisting, with each of many spots hosting one individual of each species and synchronised life cycles:

1. Individuals of A and B interact. Their investments into mutualism respond dynamically to one another:

$$\begin{aligned} \frac{da_{\mathrm{A},t}}{dt} &= a_0 - a_{\mathrm{A},t} + z_{\mathrm{A}}\, a_{\mathrm{B},t}, \\ \frac{da_{\mathrm{B},t}}{dt} &= a_0 - a_{\mathrm{B},t} + z_{\mathrm{B}}\, a_{\mathrm{A},t}, \end{aligned} \tag{2}$$

   where $a_{i,t}$ is the investment of species $i \in \{\mathrm{A}, \mathrm{B}\}$ at behavioural time t, and z_i is the evolving trait of species i capturing responsiveness (reciprocity).

2. After interactions, individuals reproduce with fecundities depending on the equilibrium investments (i.e. on $a_{\mathrm{A}} = a_{\mathrm{A},t}$ and $a_{\mathrm{B}} = a_{\mathrm{B},t}$ as $t \to \infty$):

$$\begin{aligned} f_{\mathrm{A}}(a_{\mathrm{A}}, a_{\mathrm{B}}) &= \big(f_0 + b_{\mathrm{A}} a_{\mathrm{B}}\big) \exp(-c_{\mathrm{A}} a_{\mathrm{A}}), \\ f_{\mathrm{B}}(a_{\mathrm{B}}, a_{\mathrm{A}}) &= \big(f_0 + b_{\mathrm{B}} a_{\mathrm{A}}\big) \exp(-c_{\mathrm{B}} a_{\mathrm{B}}), \end{aligned} \tag{3}$$

   where b_i and c_i scale the benefits and costs of mutualism, and f_0 is baseline fecundity. Mutualism is facultative provided that $f_0 > 0$ (i.e. individuals can reproduce without it). After reproduction, all adults die.
3. Offspring of each species compete randomly within species for breeding spots.

- How do z_{A} and z_{B} coevolve?
- What are the conditions for mutualism to evolve (i.e. for $z_{\mathrm{A}}^{*} > 0$ and $z_{\mathrm{B}}^{*} > 0$ to both be convergence stable)?
- Can a cheater strain of one species invade a population at the convergence stable equilibrium $(z_{\mathrm{A}}^{*}, z_{\mathrm{B}}^{*})$?
- What changes if mutualism is obligate ?

Project 4: What can lead to the evolution of accelerated senescence?

One hypothesis for the evolution of senescence is **antagonistic pleiotropy**: the same trait can improve performance at young ages but reduce it later in life (or vice versa), and selection may prioritise performance in some age classes over others. What can affect how strongly antagonistic pleiotropy shapes life-history evolution?

Proposed framework: Consider a population where individuals can live up to two years, and express a trait z that affects fecundity at both ages. The life cycle is:

1. Individuals of both ages reproduce with fecundity :

$$b_1(z) = K(x)\, f_1(z), \qquad b_2(z) = K(x)\, f_2(z),$$

   where $K(x)$ is the establishment probability ensuring demographic stationarity of a monomorphic population (i.e. such that $R_0(x, x) = 1$).

1. (continued) When $f_1(z)$ and $f_2(z)$ are maximised for different trait values z, the trait has antagonistic effects across ages.
2. Individuals of age 1 survive to age 2 with probability $s_1 \in [0, 1]$. Individuals of age 2 die.

Questions that can be explored

- How does z evolve when there is conflict between age 1 and age 2?
- How does this change with survival to age 2 (s_1)?
- How would these results extend with more than two age classes?
- What if z affected juvenile and adult survival instead of fecundity?
- How could we modify the model in a simple way to consider the effect of mutation accumulation on senescence evolution?

Project 5: What drives the evolution of dispersal?

Dispersal is often dangerous and costly. Why then leave a good patch where one's parents reproduced successfully, and face the risks of dispersal?

Proposed framework: Consider a population subdivided into groups of size n, with a Moran life cycle and island model of dispersal:

1. Individuals reproduce (all with the same fecundity), producing a large number of offspring.
2. Each offspring disperses with probability z or remains in its natal patch with probability $1 - z$. Dispersers survive with probability $1 - c_{\mathrm{d}}$, where c_{d} is the cost of dispersal.
3. One randomly chosen adult per group dies, and offspring compete locally for the vacant spot.

Questions that can be explored

- How does the evolution of dispersal z change the cost of dispersal c_d and group size n?
- Is dispersal a selfish or an altruistic behaviour?
- What is relatedness at evolutionary equilibrium, and what does this imply about the environments where prosocial behaviours are expected to evolve?

Project 6: When does temporal heterogeneity favour polymorphism?

Bet-hedging in temporally variable environments often disfavors polymorphism, since no lineage can risk disappearing in an unfavourable year. Yet mechanisms such as seed banks or adult survival can buffer these risks and help lineages persist through bad years. Can this promote polymorphism?

Proposed framework: Consider a well-mixed population of large and constant size where the environment alternates between two states each year (e.g. wet vs dry, hot vs cold), with the following life cycle:

1. Individuals reproduce, producing many offspring. Fecundity in environment $i \in \{1, 2\}$ is
$$\exp\left(-\frac{(z-\theta_i)^2}{2\sigma_i^2}\right),$$
maximised at θ_1 in environment 1 and at θ_2 in environment 2, with selection strength set by σ_i.

2. Each adult survives to the next year with probability s, or dies with probability $1 - s$. Empty spots are filled by offspring competing randomly.
3. The environment switches from state 1 to 2 with probability p_{12}, and from 2 to 1 with probability p_{21}.

Questions that can be explored

- How does adult survival (s) affect the scope for evolutionary branching and polymorphism ?
- How do the rate and predictability of environmental change (p_{12}, p_{21}) influence diversification ?
- When branching occurs, are both morphs perfectly specialised to each environment ?