

Chapter 2. A mean-field individual-based model

2.1 General form and introduction

‘Modelling is a way of enforcing constraints on otherwise wishful thinking.’

Giulio Ruffini

In this chapter a mean-field model of two coupled differential equations of diverse communities is considered. The model is defined in order to establish whether traits of individuals have an important role in determining community diversity. The model is very simple, containing only a few basic mechanisms, and was designed to give general clues that might guide more detailed and realistic models. In this model, space is not defined explicitly. Instead, interactions between individuals with different trait values are explored. In the model, individuals are described by three physiological traits: lifetime, time to reproduction, and number of progeny produced per unit time. The model of a population such that the time to reproduction varies between individuals (*i.e.* there exists diversity in the time of reproduction) is now defined.

The biological system under consideration is a population of plants, since this work was conducted as a part of a project investigating the diversity of Scottish grasslands. Suppose there is a population consisting of F adult plants and S seeds. Suppose further that adult individuals reproduce at intervals of $1/\lambda$ (time to reproduction), *i.e.* λ is the rate of reproduction. Assume that the seedlings compete with each other. The aim is to express the density dependence of seed germination as a function of the seed population. Call the number of germinated seeds in one season G . Then define G as follows (Harper 1977):

$$G = \frac{\lambda S}{1 + KS}$$

where K is a constant determining the strength of competition (competition increases as K increases). The shape of the curve is shown in Figure 2.1.

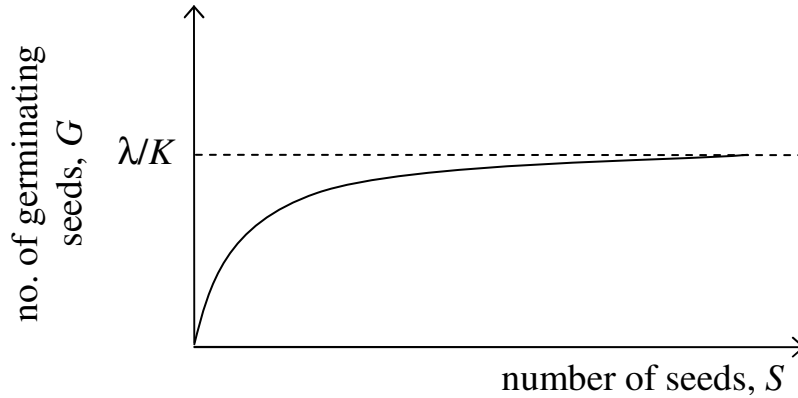


Figure 2.1 The number of germinating seeds as a function of the total number of seeds. This relation expresses competition that seeds experience in the presence of other seeds.

Suppose that within the population, there are individuals with a range of reproduction rate values $(0, \lambda_c)$, where λ_c is the upper limit of λ . First, suppose that each seed competes with all other seeds. Then S and G are functions of λ . For a given value of λ , $S(\lambda)d\lambda$ is the number of seeds corresponding to individuals with reproduction rates in the range λ to $(\lambda+d\lambda)$, and $G(\lambda)d\lambda$ is the number of those that germinate. In this case

$$G(\lambda) = \frac{\lambda S(\lambda)}{1 + K \int_0^{\lambda_c} S(l) dl}$$

where the integral represents the total number of seeds in a population.

Other competition scenarios can be expressed by introducing a kernel into the integral in order to characterise the extent to which seeds with different reproduction rates contribute to competition:

$$G(\lambda) = \frac{\lambda S(\lambda)}{1 + K \int_0^{\lambda_c} \kappa(l, \lambda) S(l) dl}$$

where $\kappa(l, \lambda)$ is the kernel.

For example, suppose that individuals with reproduction rate λ_i only have to compete with individuals of higher reproduction rate to reach maturity. Then the kernel can be described as:

$$\kappa(l, \lambda) = \begin{cases} 0 & \text{if } l < \lambda \\ 1 & \text{if } l \geq \lambda \end{cases}$$

and

$$G(\lambda_i) = \frac{\lambda_i S(\lambda_i)}{1 + K \int_{\lambda_i}^{\lambda_c} S(l) dl} . \quad (2.1)$$

Now consider a population consisting of seeds and adults, with seeds being produced at rates in the interval $(0, \lambda_c)$. Let $S(\lambda, t)d\lambda$ be the number of seeds in the population corresponding to individuals with reproduction rate in the range λ to $(\lambda+d\lambda)$, and let $F(\lambda, t)d\lambda$ be the corresponding number of adults, at a given time t . The evolution of the adult population over time can be described as

$$\frac{\partial F}{\partial t} = G(\lambda) - aF(\lambda, t) \quad (2.2)$$

where a is the death rate of adult individuals. Substituting (2.1) into (2.2),

$$\frac{\partial F}{\partial t} = \underbrace{\frac{\lambda S(\lambda, t)}{1 + K \int_0^{\lambda_c} \kappa(l, \lambda) S(l, t) dl}}_{\text{germinated seeds}} - \underbrace{aF(\lambda, t)}_{\text{adult death}} . \quad (2.3)$$

To describe the evolution of the seed population over time, it is necessary to define the process of geneflow. Consider the simple case when all adults cross with all other adults (*e.g.* by pollen mixing). Also suppose that at each crossing there is a probability $\rho(\lambda | x, y)$ that a seed of an individual with reproduction rate λ will be produced by two parents with reproduction rates x and y , respectively. Then the number of seeds $B(\lambda, t)d\lambda$ produced at time t with reproduction rate in the range λ to $(\lambda+ d\lambda)$ can be described by

$$B(\lambda, t) = b \frac{1}{2} \int_0^{\lambda_c} \int_0^{\lambda_c} \rho(\lambda | x, y) F(x, t) F(y, t) dx dy$$

where b is the number of seeds produced per unit time when an adult with reproduction rate x crosses with an adult with reproduction rate y .

The more general case can be considered when not all adults cross with each other. Suppose a function $Q[F(x,t), F(y,t)]$ describes the frequency of crossing for two individuals with reproduction rates x and y . Then $B(\lambda, t)$ can be defined as follows:

$$B(\lambda, t) = b \int_0^{\lambda_c} \int_0^{\lambda_c} \rho(\lambda | x, y) Q[F(x, t), F(y, t)] dx dy \quad (2.4)$$

The change in seed population over time can then be described as:

$$\frac{\partial S}{\partial t} = B(\lambda, t) - c\lambda S(\lambda, t) \quad (2.5)$$

where $c\lambda$ is the proportion of seeds that die and become adult. Substituting (2.4) into (2.5),

$$\frac{\partial S}{\partial t} = \underbrace{b \int_0^{\lambda_c} \int_0^{\lambda_c} \rho(\lambda | x, y) Q[F(x, t), F(y, t)] dx dy}_{\text{rate of production of seeds}} - \underbrace{c\lambda S(\lambda, t)}_{\text{rate of seed death and germination}} \quad (2.6)$$

A coupled system of differential equations can now be described by combining equations (2.3) and (2.6) as follows:

$$\begin{cases} \frac{\partial F}{\partial t} = \frac{\lambda S(\lambda, t)}{1 + K \int_0^{\lambda_c} \kappa(l, \lambda) S(l, t) dl} - aF(\lambda, t) \\ \frac{\partial S}{\partial t} = b \int_0^{\lambda_c} \int_0^{\lambda_c} \rho(\lambda | x, y) Q[F(x, t), F(y, t)] dx dy - c\lambda S(\lambda, t) \end{cases} \quad (2.7)$$

This system can be non-dimensionalised as follows. Let $\tau = at$, then

$$\begin{cases} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau) / a}{1 + K \int_0^{\lambda_c} \kappa(l, \lambda) S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = b/a \int_0^{\lambda_c} \int_0^{\lambda_c} \rho(\lambda | x, y) Q[F(x, \tau), F(y, \tau)] dx dy - c\lambda S(\lambda, \tau) / a \end{cases} \quad (2.8)$$

Define $\lambda^* = \lambda / \lambda_c$, $l^* = l / \lambda_c$, $x^* = x / \lambda_c$, and $y^* = y / \lambda_c$. Then

$$\left\{ \begin{array}{l} \frac{\partial F}{\partial \tau} = \frac{\lambda^* S(\lambda^* \lambda_c, \tau) \lambda_c / a}{1 + K \lambda_c \int_0^1 \kappa(l^* \lambda_c, \lambda^* \lambda_c) S(l^* \lambda_c, \tau) dl^*} - F(\lambda^* \lambda_c, \tau) \\ \frac{\partial S}{\partial \tau} = b / a \int_0^1 \int_0^1 \rho(\lambda^* \lambda_c | x^* \lambda_c, y^* \lambda_c) Q[F(x^* \lambda_c, \tau), F(y^* \lambda_c, \tau)] dx^* dy^* - c \lambda^* S(\lambda^* \lambda_c, \tau) \lambda_c / a \end{array} \right. \quad (2.9)$$

Let $S^*(\lambda^*, \tau) = S(\lambda^* \lambda_c, \tau)$, $F^*(\lambda^*, \tau) = F(\lambda^* \lambda_c, \tau)$, $\kappa^*(l^*, \lambda^*) = \kappa(l^* \lambda_c, \lambda^* \lambda_c)$, and

$$\rho^*(\lambda^* | x^*, y^*) = \rho(\lambda^* \lambda_c | x^* \lambda_c, y^* \lambda_c).$$

Let

$$\frac{\lambda_c}{a} = R^* = \frac{\text{lifetime}}{\text{minimum time to reproduction}}, \quad (2.10)$$

$$\begin{aligned} \frac{b}{a} = P^* &= \frac{(\text{lifetime})(\text{number of offspring})}{\text{time}} \\ &= \text{total number of offspring produced by an individual.} \end{aligned} \quad (2.11)$$

Then the system becomes:

$$\left\{ \begin{array}{l} \frac{\partial F^*}{\partial \tau} = \frac{R^* \lambda^* S^*(\lambda^*, \tau)}{1 + K \lambda_c \int_0^1 \kappa^*(l^*, \lambda^*) S^*(l^*, \tau) dl^*} - F^*(\lambda^*, \tau) \\ \frac{\partial S^*}{\partial \tau} = P^* \int_0^1 \int_0^1 \rho^*(\lambda^* | x^*, y^*) Q[F^*(x^*, \tau), F^*(y^*, \tau)] dx^* dy^* - R^* c \lambda^* S^*(\lambda^*, \tau) \end{array} \right. \quad (2.12)$$

2.2 A model with clonal reproduction and hierarchical competition

2.2.1 Model definition

Consider a simplification of (2.12) where reproduction is clonal:

$$\left\{ \begin{array}{l} \frac{\partial F^*}{\partial \tau} = \frac{R^* \lambda^* S^*(\lambda^*, \tau)}{1 + K \lambda_c \int_0^1 \kappa^*(l^*, \lambda^*) S^*(l^*, \tau) dl^*} - F^*(\lambda^*, \tau) \\ \frac{\partial S^*}{\partial \tau} = P^* F^*(\lambda^*, \tau) - R^* c \lambda^* S^*(\lambda^*, \tau) \end{array} \right. \quad (2.13)$$

To reduce the number of parameters, let $S^{**}(\lambda^*, \tau) = \lambda_c K S^*(\lambda^*, \tau)$ and let

$F^{**}(\lambda^*, \tau) = \lambda_c K F^*(\lambda^*, \tau) / R^*$. The kernel function does not change since

$$\lambda_c K \int_0^1 \kappa^*(l^*, \lambda^*) S^*(l^*, \tau) dl^* = \int_0^1 \kappa^*(l^*, \lambda^*) K \lambda_c S^*(\lambda^*, \tau) dl^* = \int_0^1 \kappa^*(l^*, \lambda^*) S^{**}(\lambda^*, \tau) dl^*$$

For convenience of notation, the superscripts * and ** on $\lambda, l, \kappa, x, y, S$ and F are left out below:

$$\begin{cases} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_0^1 \kappa(l, \lambda) S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{1}{R^*} \frac{\partial S}{\partial \tau} = P^* F(\lambda, \tau) - c \lambda S(\lambda, \tau) \end{cases} \quad (2.14)$$

Let $P = R^* P^*$ and $C = R^* c$. Then (2.14) becomes:

$$\begin{cases} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_0^1 \kappa(l, \lambda) S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = P F(\lambda, \tau) - C \lambda S(\lambda, \tau) \end{cases} \quad (2.15)$$

Considered boundary conditions are: $\lambda \in [0, 1]$ and $F(0, \tau) = S(0, \tau) = F(1, \tau) = S(1, \tau) = 0$.

This means that there are no individuals that grow at a rate $\lambda = 0$, and no individuals that grow at a rate $\lambda = 1$ (since this was defined as the upper limit of λ). Now several forms of $\kappa(l, \lambda)$ can be considered.

First, consider a simple form of the kernel $\kappa(l, \lambda)$, which expresses strictly hierarchical competition, *i.e.* an individual competes equally with all individuals that grow as fast or faster than it does:

$$\kappa(l, \lambda) = \begin{cases} 0 & \text{if } l < \lambda \\ 1 & \text{if } l \geq \lambda \end{cases}$$

The system (2.15) becomes:

$$\begin{cases} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_{\lambda}^1 S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = P F(\lambda, \tau) - C \lambda S(\lambda, \tau) \end{cases}$$

Other forms of κ will be considered in section 2.5.

$$\text{Let } H(\lambda, \tau) = 1 + \int_{\lambda}^1 S(l, \tau) dl .$$

This means that the system can be rewritten as

$$\begin{cases} \frac{\partial F}{\partial \tau} = -\lambda \frac{\partial H}{\partial \lambda} \frac{1}{H} - F(\lambda, \tau) \\ -\frac{\partial^2 H}{\partial \lambda^2} = PF + C\lambda \frac{\partial H}{\partial \lambda} \end{cases} \quad (2.16)$$

Here,

$$S(\lambda, \tau) = -\frac{\partial H}{\partial \lambda} . \quad (2.17)$$

$H(\lambda, \tau)$ has several constraints. First, since $S(1, \tau) = 0$ is a boundary condition, this means that

$$H(1, \tau) = 1. \quad (2.18)$$

Also, since $S(\lambda, \tau)$ must be non-negative,

$$\frac{\partial H}{\partial \lambda} \leq 0 \text{ on } [0, 1].$$

And if $S(\lambda, \tau)$ must be positive (*e.g.* for a non-zero steady state),

$$\frac{\partial H}{\partial \lambda} < 0 \text{ on } [0, 1]. \quad (2.19)$$

2.2.2 Steady states and stability

Let $H(\lambda, \tau) = h(\lambda) + h(\lambda, \tau)$ and $F(\lambda, \tau) = f(\lambda) + f(\lambda, \tau)$ where (f, h) is a steady state, *i.e.*

$$-\lambda \frac{\partial h}{\partial \lambda} \frac{1}{h} - f = 0 \quad (2.20)$$

and

$$Pf + C\lambda \frac{\partial h}{\partial \lambda} = 0 \quad (2.21)$$

Now (2.20) implies that

$$\lambda \frac{\partial h}{\partial \lambda} = -hf \quad (2.22)$$

Plugging this in into (2.21)

$$Pf - Chf = 0$$

or

$$f(P - Ch) = 0$$

This means that either $f = 0$ or $h = P/C$ or both.

$$\text{If } h = P/C \quad (2.23)$$

then

$$\begin{aligned} f &= -\lambda \frac{\partial h}{\partial \lambda} \frac{1}{h} \\ &= -\lambda \frac{\partial(P/C)}{\partial \lambda} \frac{C}{P}. \end{aligned} \quad (2.24)$$

Until this point no conditions on $\frac{P}{C}$ were imposed. However, (2.24) implies that the

ratio $\frac{P}{C}$ must be a function of λ . Moreover, the steady state of the system depends on

this ratio and its derivative. Two constraints on $\frac{P}{C}(\lambda)$ can be derived. First, from (2.18)

and (2.19) $\frac{P}{C}(1) = 1$. Second,

$$\frac{\partial(P/C)}{\partial \lambda} < 0 \quad (2.25)$$

on $[0, 1]$. This implies that $\frac{P}{C}(\lambda)$ is a decreasing function of λ . Now, $\frac{P}{C}(\lambda) = \frac{b}{ca}(\lambda)$.

Therefore, inequality (2.25) imposes constraints on the relationship between the physiological parameters necessary for coexistence. The inequality requires the ratio of the number of offspring (per unit time) and the product of adult death rate and juvenile death and maturation rates to be a decreasing function.

Boundary conditions also imply that since $\frac{\partial h(1)}{\partial \lambda} = 0$, $\frac{\partial(P/C)(1)}{\partial \lambda} = 0$.

Note that $f = 0$ then (2.22) implies that $\frac{\partial h}{\partial \lambda} = 0$, i.e. $h = h_0$ where h_0 is a constant.

Since a steady state with seeds and no flowers is impossible, h_0 is 1, which corresponds to $s_0 = 0$. Therefore, this state represents extinction of seeds and flowers. Also, note

that if $\frac{P}{C}$ is a constant, then $\frac{\partial(P/C)}{\partial \lambda} = 0$, and therefore $f=0$.

Therefore, steady states are

$$(f, h) \quad \text{and} \quad (0, h_0).$$

It was not possible to conduct a full analytical treatment of the linear stability analysis (Appendix A). Therefore, the stability of the system was explored numerically.

2.2.3 Numerical simulation results

In order to explore the stability of steady states described in the previous section, the system was simulated numerically. An ODE solver (ordinary differential equation solver) by Hairer *et al.* (1993) was used. The solver simulates the evolution of the system from a given initial state. It uses the Runge-Kutta method of order 8 with step size control and dense output.

In the system under consideration, both $F(\lambda, \tau)$ and $S(\lambda, \tau)$ are defined for values of λ in the range (0, 1). To represent the distributions of $F(\lambda, \tau)$ and $S(\lambda, \tau)$ along λ , the system was discretised along λ . To discretise λ , the interval was divided into even λ -steps, $\Delta\lambda$.

The continuous function $S(\lambda, \tau)$ was then discretised to become $S(\lambda_i, \tau)$ where $\lambda_i = 0,$

$\Delta\lambda, 2\Delta\lambda, \dots, 1$. Similarly, $F(\lambda, \tau)$ was discretised. To represent $\int_{\lambda}^1 S(l, \tau) dl$ the

trapezoidal approximation was used. That is $\int_{\lambda}^1 S(l, \tau) dl$ was approximated by

$$\Delta\lambda \left[\frac{1}{2} S(\lambda_i, \tau) + \sum_{j=i+1}^{n-1} S(j, \tau) + \frac{1}{2} S(1, \tau) \right]$$

where λ from the integral was in the interval $(\lambda_i, \lambda_i + \Delta\lambda)$.

Therefore, the continuous system was replaced by a system of equations

$$\left\{ \begin{array}{l} \frac{dF(\lambda_i, \tau)}{d\tau} = \frac{\lambda_i S(\lambda_i, \tau)}{1 + \Delta\lambda \left[\frac{1}{2} S(\lambda_i, \tau) + \sum_{j=j+1}^{n-1} S(\lambda_j, \tau) + \frac{1}{2} S(1, \tau) \right]} - F(\lambda_i, \tau) \\ \frac{dS(\lambda_i, \tau)}{d\tau} = PF(\lambda_i, \tau) - C\lambda_i S(\lambda_i, \tau) \end{array} \right.$$

First, the steady state $(f, h) = (0, h_0)$ is explored. This corresponds to the steady state $(f, s) = (0, 0)$. The stability analysis revealed that this steady state is a stable node if

$\frac{P}{C}(\lambda) < 1$. To confirm this, simulations were performed with $\frac{P}{C}(\lambda) < 1$: case 1) $P=0.2$, and $C=0.5$; case 2) $P=4\lambda^2$ and $C=0.5$. Two sets of initial conditions were used: 1) $(F(\lambda), S(\lambda)) = (1, 1)$ and 2) $F(\lambda)$ and $S(\lambda)$ picked randomly from the range $(0, 100)$. In all simulations, the system immediately settled to the $(0, 0)$ state.

To explore the stability of the non-zero steady state, two functions of $P(\lambda)$ were used for simulations:

Case 1: $P(\lambda) = (\lambda - 1)^2 + 1.5$ and $C=1.5$. Substituting for $\frac{P}{C}(\lambda)$ in (2.17) and (2.23),

$$s(\lambda) = \frac{4}{3}(1 - \lambda),$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.24),

$$f(\lambda) = 2 \frac{\lambda - \lambda^2}{(\lambda - 1)^2 + 1.5}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing

on the interval $(0,1)$, and $\frac{P}{C}(1) = 1$.

Case 2: $P(\lambda) = \frac{1}{2\lambda - \lambda^2 + 1} + 1$ and $C=1.5$, which meant that the analytical non-zero

steady state was the following.

Substituting for $\frac{P}{C}(\lambda)$ in (2.17) and (2.23),

$$s(\lambda) = \frac{4}{3} \frac{(1 - \lambda)}{(2\lambda - \lambda^2 + 1)^2},$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.24),

$$f(\lambda) = 2 \frac{\lambda - \lambda^2}{(2\lambda - \lambda^2 + 1)^2 \left(\frac{1}{2\lambda - \lambda^2 + 1} + 1 \right)}$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing on the interval (0,1), and $\frac{P}{C}(1) = 1$.

To explore the stability of the steady state, experiments were conducted with $F(\lambda)$ and $S(\lambda)$ at various values away from the analytically determined steady state. The simulations were performed with the following initial states:

- 1) setting $F(\lambda)$ to the steady state values $f(\lambda)$, and setting $S(\lambda)$ to values a) $s(\lambda) \pm 0.001 s(\lambda)$; b) $s(\lambda) \pm 0.01 s(\lambda)$; c) $s(\lambda) \pm 0.1 s(\lambda)$; d) $s(\lambda) \pm 0.5 s(\lambda)$; if the assigned value was negative, then its absolute values was used (since $F(\lambda)$ and $S(\lambda)$ cannot take on negative values);
- 2) setting $S(\lambda)$ to the steady state values $s(\lambda)$, and setting $F(\lambda)$ to values a) $f(\lambda) \pm 0.001 f(\lambda)$; b) $f(\lambda) \pm 0.01 f(\lambda)$; c) $f(\lambda) \pm 0.1 f(\lambda)$; d) $f(\lambda) \pm 0.5 f(\lambda)$; if the assigned value was negative, then its absolute values was used (since $F(\lambda)$ and $S(\lambda)$ cannot take on negative values);
- 3) $F(\lambda)=S(\lambda)=1$ on $\lambda \in (0, 1)$;
- 4) $F(\lambda)$ and $S(\lambda)$ assigned random values from 0 to 100.

The λ -step, $\Delta\lambda$, was set to 0.01. The simulations were not sensitive to the value of λ -step as long as λ -step was below 0.1. In all cases, the simulations converged to the steady state before 400,000 time steps. An example of a simulation for the initial condition of 1 is presented in Figures 2.2 and 2.3, which show the distribution of $F(\lambda)$ and $S(\lambda)$ at four different time points (plots 2.2 and 2.3 a, b, c, and d) as the system approached the predicted steady state. Figure 2.4 shows sample phase plane plots for two values of λ ($\lambda=0.9$ and $\lambda=0.7$). The phase plane plots show oscillatory behaviour that is more pronounced for smaller values of λ . Another phase plane plot is shown in Figure 2.5, for the initial state when $S(\lambda)$ was set to the steady state $s(\lambda)$, and $F(\lambda)$ was set to $F(\lambda) \pm 0.5 f(\lambda)$ (with constraint that it is always positive). The plot shows oscillatory behaviour, as in Figure 2.4. However, in this case the oscillatory behaviour is not as uniform, possibly due to the random variation of the initial condition for $F(\lambda)$. The same behaviour is observed for all values of λ , but the oscillations are more frequent for smaller values of λ .

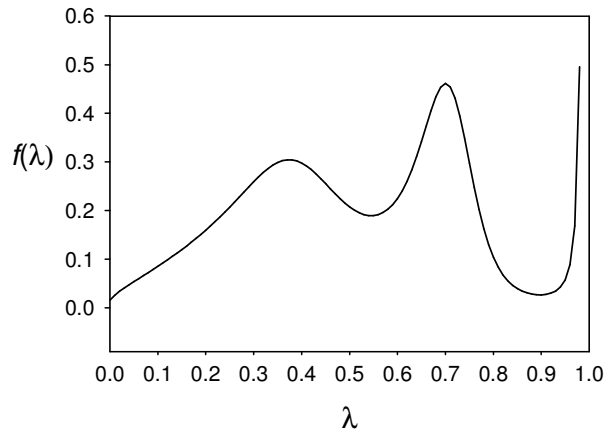


Fig. 2.2 a) time step 300;

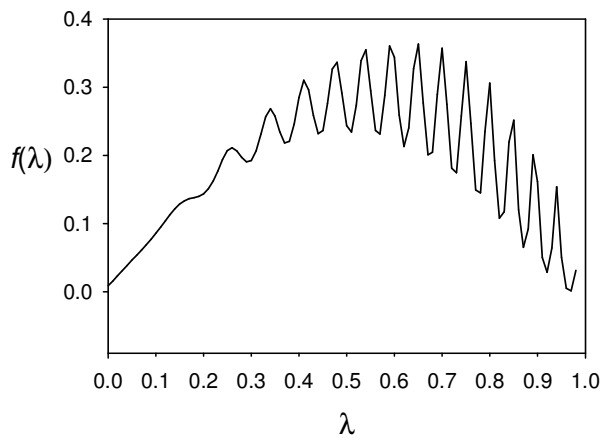


Fig. 2.2 b) time step 1,000;

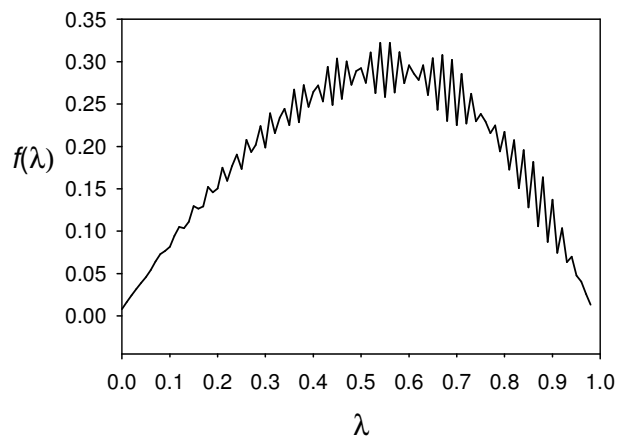


Fig. 2.2 c) time step 100,000;

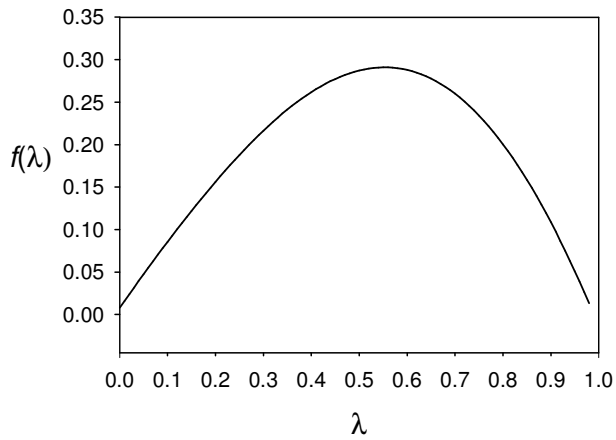


Fig. 2.2 d) time step 400,0000 – steady state.

Figure 2.2 Simulation of the distribution of the fecund individuals across λ . The simulation evolved through states shown in a) and b) towards c) which is the steady state predicted by analysis. Initial conditions for the simulation were: $F(\lambda)=1$, $S(\lambda)=1$ for $0 < \lambda < 1$; $F(\lambda)=0$, $S(\lambda)=0$ for $\lambda=1$ (the upper limit of λ values). However, the simulation outcome did not depend on the initial conditions.

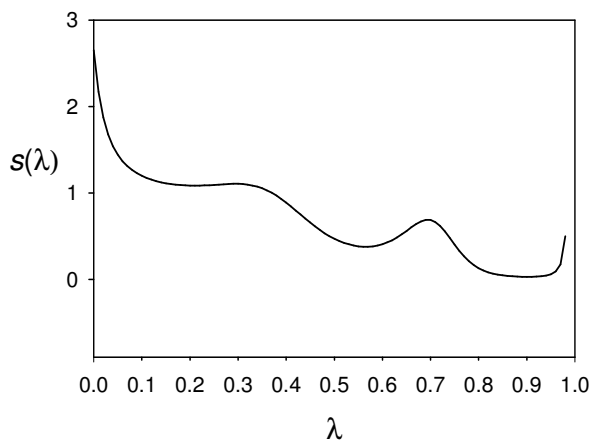


Fig. 2.3 a) time = 300;

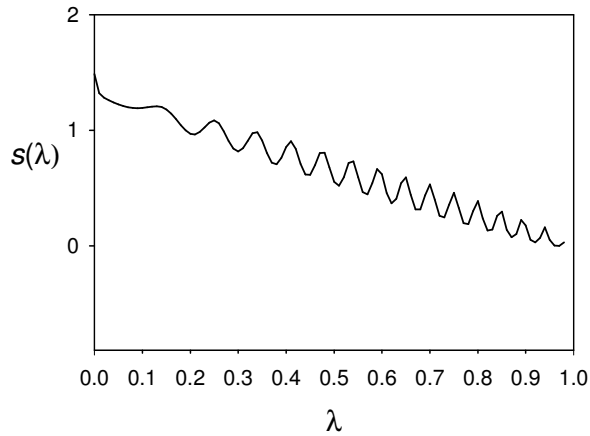


Fig. 2.3 b) time step=10,000;

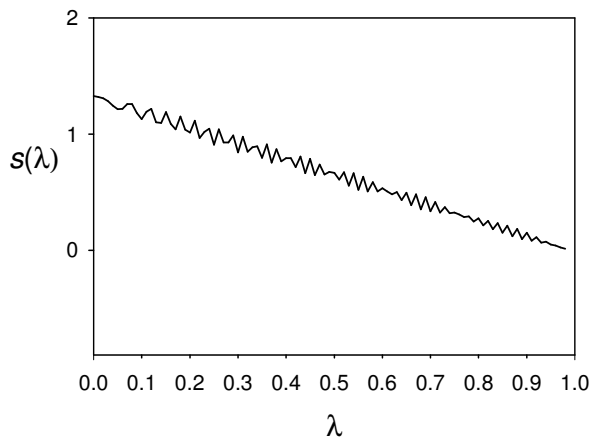


Fig. 2.3 c) time step 100,000;

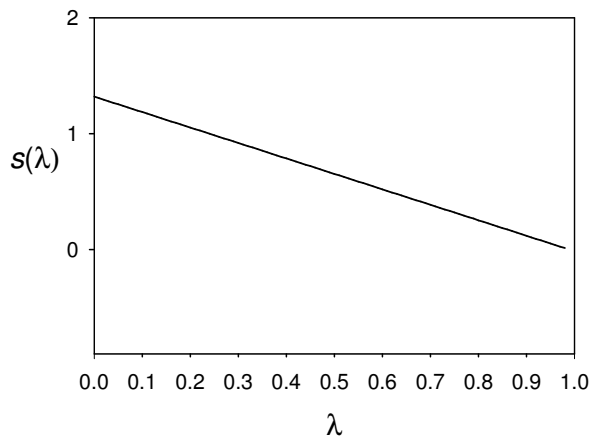


Fig. 2.3 d) time step 400,000 – steady state.

Figure 2.3 Simulation of the distribution of seeds across λ . The simulation evolved through states shown in a, b and c towards d) which is the steady state predicted by analysis. Initial conditions for the simulation: $F(\lambda)=1, S(\lambda)=1$ for $0 < \lambda < 1$; $F(\lambda)=0, S(\lambda)=0$ for $\lambda=1$ (the upper limit of λ values). However, the simulation outcome did not depend on the initial conditions.

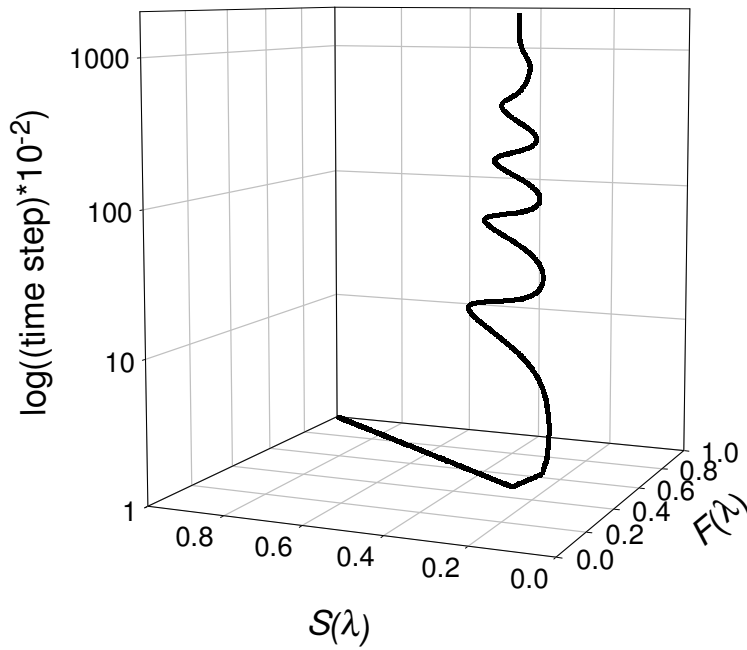


Fig. 2.4 a) Phase plane plot for $F(\lambda)$ and $S(\lambda)$ at $\lambda=0.9$. Note that time is shown on log scale.

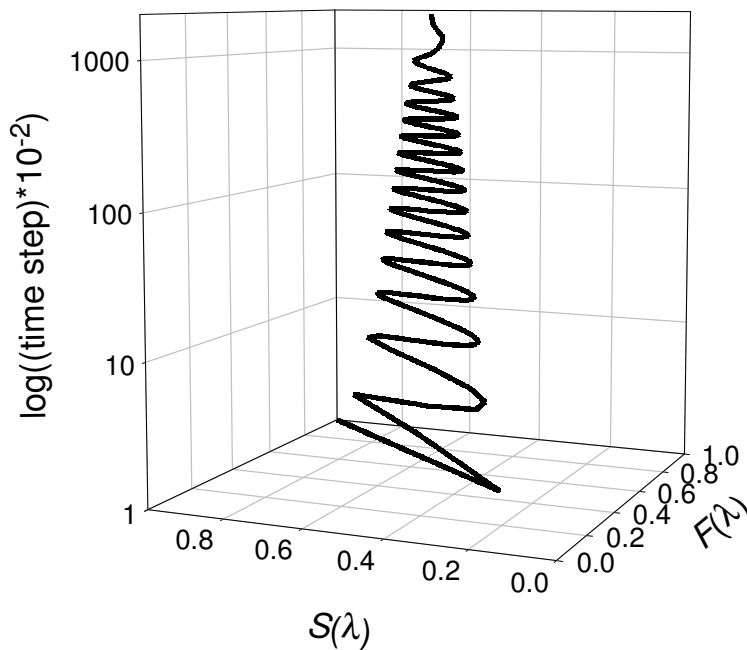


Fig. 2.4 b) Phase plane plot for $F(\lambda)$ and $S(\lambda)$ at $\lambda=0.7$. The dynamics are the same as in the phase plant plot for $\lambda=0.9$, but with more fluctuations. In general, for smaller λ values, there are more fluctuations than for larger λ .

Figure 2.4 Phase plane plots for $F(\lambda)$ and $S(\lambda)$ observed in the simulations with initial state $(1, 1)$.

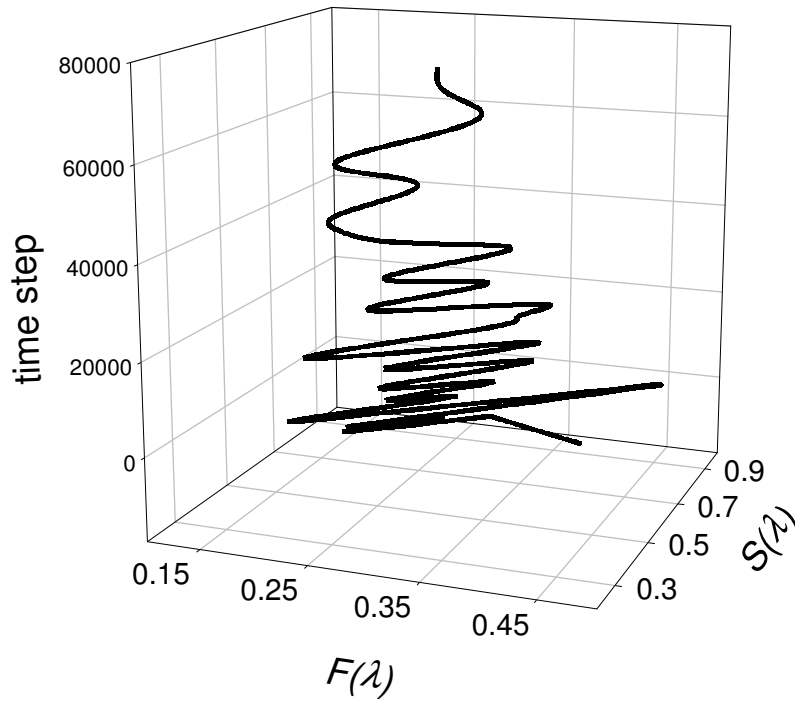


Figure 2.5 Phase plane plots for $F(\lambda)$ and $S(\lambda)$ observed in the simulations with initial state $(f(\lambda) \pm 0.5f(\lambda), s(\lambda))$.

2.3 Implications for diversity maintenance

The model was formulated to explore the connection between the basic physiological traits of individuals in a community and community diversity. The results show that a relationship among the individual traits is necessary in order to maintain diversity in the system. In particular, $\frac{P}{C}(\lambda) = \frac{b}{ca}(\lambda)$, the ratio between the number of offspring (per unit time) b and the product of death rate of adult plants, a , and death and maturation rate of juvenile plants, c , had to be a decreasing function of the reproduction rate λ . In other words, plants that reproduced at a smaller rate had to have a bigger number of offspring to death and maturation rates ratio (Figure 2.6). This shows that the trade-off among traits of individuals needs to be of a particular form in order for community diversity to exist.

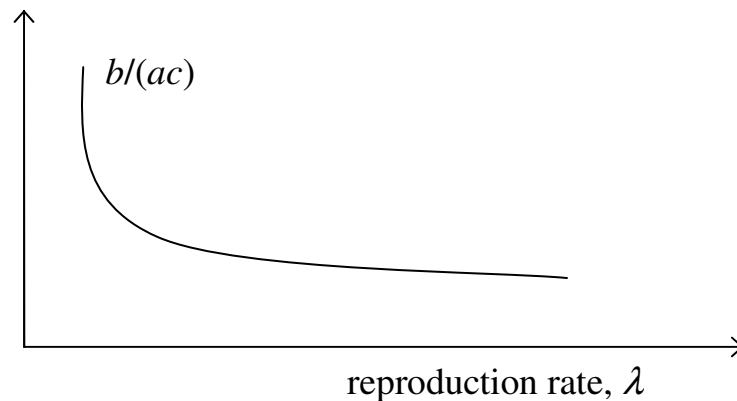


Figure 2.6 Ratio of number of offspring (per unit time), b , to the product of adult death rate, a , and juvenile death and maturation rate, c , is a decreasing function of the reproduction rate λ .

In addition to determining community diversity, the form of the trade off also determined the relative abundance of individuals with different trait values. The stable steady states of the systems were shown to be a function of the ratio $\frac{b}{ca}(\lambda)$. Therefore, the shape of function determined the final shape of the population distribution (Figure 2.7).

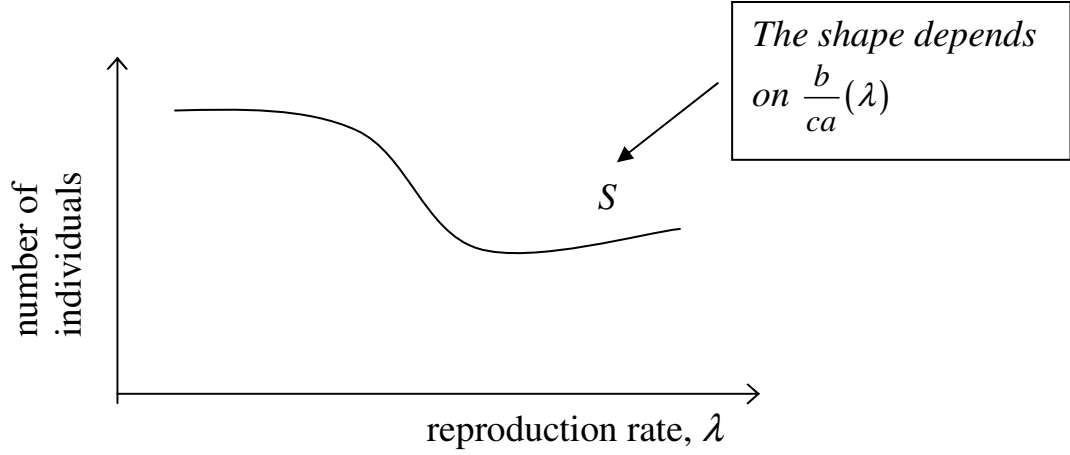


Figure 2.7 Example of the distribution of $S(\lambda)$ (the number of seeds in a population) as a function of the reproduction rate λ . $S(\lambda)$ is a function of $\frac{b}{ca}(\lambda)$.

2.4 A model with genetic coupling and hierarchical competition

2.4.1 Model definition

This section explores the effect of genetic coupling on the system requirements for diversity. Returning to eq. (2.12)

$$\left\{ \begin{array}{l} \frac{\partial F^*}{\partial \tau} = \frac{R^* \lambda^* S^*(\lambda^*, \tau)}{1 + K \lambda_c \int_0^1 \kappa^*(l^*, \lambda^*) S^*(l^*, \tau) dl^*} - F^*(\lambda^*, \tau) \\ \frac{\partial S^*}{\partial \tau} = P^* \int_0^1 \int_0^1 \rho^*(\lambda^* | x^*, y^*) Q[F^*(x^*, \tau), F^*(y^*, \tau)] dx^* dy^* - R^* c \lambda^* S^*(\lambda^*, \tau) \end{array} \right.$$

To reduce the number of parameters, let $S^{**}(\lambda^*, \tau) = \lambda_c K S^*(\lambda^*, \tau)$ and

$$F^{**}(\lambda^*, \tau) = \frac{\lambda_c K F^*(\lambda^*, \tau)}{R^*}. \text{ The kernel function does not change since}$$

$$\lambda_c K \int_0^1 \kappa^*(l^*, \lambda^*) S^*(l^*, \tau) dl^* = \int_0^1 \kappa^*(l^*, \lambda^*) K \lambda_c S^*(\lambda^*, \tau) dl^* = \int_0^1 \kappa^*(l^*, \lambda^*) S^{**}(\lambda^*, \tau) dl^*$$

Then the system can be rewritten as

$$\left\{ \begin{array}{l} \frac{\partial F^{**}}{\partial \tau} = \frac{\lambda^* S^{**}(\lambda^*, \tau)}{1 + \int_0^1 \kappa^*(l^*, \lambda^*) S^{**}(l^*, \tau) dl^*} - F^{**}(\lambda^*, \tau) \\ \frac{\partial S^{**}}{\partial \tau} = (R^*)^2 P^* \int_0^1 \int_0^1 \rho^*(\lambda^* | x^*, y^*) Q[F^{**}(x^*, \tau), F^{**}(y^*, \tau)] dx^* dy^* - R^* c \lambda^* S^{**}(\lambda^*, \tau) \end{array} \right.$$

Let $P = (R^*)^2 P^*$ and $C = cR^*$. For clarity of notation, eliminate the subscripts * and ** on $\lambda, l, \kappa, x, y, S$ and F . Then:

$$\left\{ \begin{array}{l} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_0^1 \kappa(l, \lambda) S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = P \int_0^1 \int_0^1 \rho(\lambda | x, y) Q[F(x, \tau), F(y, \tau)] dx dy - C \lambda S(\lambda, \tau) \end{array} \right.$$

Consider the form of the kernel from section 2.2.1. Then the system becomes

$$\left\{ \begin{array}{l} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_{\lambda}^1 S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = P \int_0^1 \int_0^1 \rho(\lambda | x, y) Q[F(x, \tau), F(y, \tau)] dx dy - C \lambda S(\lambda, \tau) \end{array} \right.$$

Let $H(\lambda, \tau) = 1 + \int_{\lambda}^1 S(l, \tau) dl$. Then the system becomes

$$\left\{ \begin{array}{l} \frac{\partial F}{\partial \tau} = -\lambda \frac{\partial H}{\partial \lambda} - F(\lambda, \tau) \\ -\frac{\partial^2 H}{\partial \lambda^2} = P \int_0^1 \int_0^1 \rho(\lambda | x, y) Q[F(x, \tau), F(y, \tau)] dx dy + C \lambda \frac{\partial H}{\partial \lambda} \end{array} \right.$$

2.4.2 Steady states and stability

Let $I(\lambda) = P \int_0^1 \int_0^1 \rho(\lambda | x, y) Q[F(x, \tau), F(y, \tau)] dx dy$.

If $(F, H) = (0, 0)$, the system is in a steady state. Let (f, h) be a non-zero steady state.

Then:

$$\begin{cases} 0 = -\lambda \frac{\partial h}{\partial \lambda} - f(\lambda, \tau) \\ 0 = I(\lambda) + C\lambda \frac{\partial h}{\partial \lambda} \end{cases}$$

Then,

$$-\lambda \frac{\partial h}{\partial \lambda} \frac{1}{h} = f(\lambda), \quad (2.26)$$

and

$$I(\lambda) = -C\lambda \frac{\partial h}{\partial \lambda}. \quad \text{with} \quad (2.27)$$

Combining (2.26) and (2.27)

$$h(\lambda) = \frac{I(\lambda)}{Cf(\lambda)}. \quad (2.28)$$

Boundary conditions state that $h(1)=1$. Therefore,

$$\frac{I(1)}{f(1)} = C. \quad (2.29)$$

Substitute (2.28) into (2.27):

$$\begin{aligned} I(\lambda) &= C\lambda \left(-\frac{1}{C} \frac{d}{d\lambda} \left(\frac{I(\lambda)}{f(\lambda)} \right) \right) \\ I(\lambda) &= -\lambda \frac{d}{d\lambda} \left(\frac{I(\lambda)}{f(\lambda)} \right) \\ I(\lambda) &= -\lambda \frac{f(\lambda)(dI(\lambda)/d\lambda) - I(\lambda)(df(\lambda)/d\lambda)}{f^2(\lambda)} \\ f^2(\lambda)I(\lambda) &= -\lambda f(\lambda) \frac{dI(\lambda)}{d\lambda} + \lambda I(\lambda) \frac{df(\lambda)}{d\lambda} \\ f^2(\lambda)I(\lambda) + \lambda f(\lambda) \frac{dI(\lambda)}{d\lambda} - \lambda I(\lambda) \frac{df(\lambda)}{d\lambda} &= 0 \quad (2.30) \end{aligned}$$

This is a Bernoulli equation, and it can be solved as follows.

First, divide (2.30) by $-\lambda I(\lambda)$:

$$\frac{I(\lambda)}{-\lambda I(\lambda)} f^2(\lambda) - \frac{\lambda dI(\lambda)}{d\lambda} \frac{1}{\lambda I(\lambda)} f(\lambda) + \frac{df(\lambda)}{d\lambda} = 0$$

and therefore

$$-\frac{1}{\lambda} f^2(\lambda) - \frac{d(\ln I(\lambda))}{d\lambda} f(\lambda) + \frac{df(\lambda)}{d\lambda} = 0 \quad (2.31)$$

$$\text{Let } v = \frac{1}{f(\lambda)}, \quad (2.32)$$

$$\text{then } \frac{dv}{d\lambda} = -\frac{(df(\lambda)/d\lambda)}{f^2(\lambda)}.$$

Now divide (2.31) by $f^2(\lambda)$.

$$-\frac{1}{\lambda} - \frac{d(\ln I(\lambda))}{d\lambda} \frac{1}{f(\lambda)} + \frac{df(\lambda)}{d\lambda} \frac{1}{f^2(\lambda)} = 0$$

which is

$$-\frac{1}{\lambda} - \frac{d(\ln I(\lambda))}{d\lambda} v - \frac{dv}{d\lambda} = 0 \text{ or}$$

$$\frac{1}{\lambda} + \frac{d(\ln I(\lambda))}{d\lambda} v + \frac{dv}{d\lambda} = 0. \quad (2.33)$$

To solve this, let $u = e^{\int \frac{d(\ln I(\lambda))}{d\lambda}}$ be an integrating factor. Multiply (2.33) by u .

$$e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} \frac{1}{\lambda} + e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} \frac{d(\ln I(\lambda))}{d\lambda} v + e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} \frac{dv}{d\lambda} = 0$$

$$\frac{d}{d\lambda} \left(e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} v \right) + \frac{1}{\lambda} e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} = 0$$

This equation has a solution

$$v = \frac{\int \frac{1}{\lambda} e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} d\lambda + q}{e^{\int \frac{d(\ln I(\lambda))}{d\lambda}}} \quad (2.34)$$

where q is a constant.

Note that

$$e^{\int \frac{d(\ln I(\lambda))}{d\lambda}} = I(\lambda) \text{ and therefore (2.34) becomes}$$

$$v = \frac{\int \frac{I(\lambda)}{\lambda} d\lambda + q}{I(\lambda)}. \text{ Using (2.32)}$$

$$f(\lambda) = \frac{I(\lambda)}{\int \frac{I(\lambda)}{\lambda} d\lambda + q}.$$

Unfortunately, a full stability analysis was intractable for this particular system and is the subject of further work. However, the above analysis shows that genetic coupling,

along with the ratio $\frac{b}{ca}(\lambda)$, determines: 1) whether or not diversity is present, and 2) the distribution of the population along values of λ .

2.5 Relaxing hierarchical competition for the model with clonal reproduction

2.5.1 Model definition

Consider a model with clonal reproduction (as in section 2.2), but in the case where competition between individuals is not strictly hierarchical; instead, an individual competes with all individuals that grow faster than it, and also some proportion of individuals that grow slower than it. This can be expressed by the kernel in the competition integral in (2.15), of the following form:

$$\kappa(l, \lambda) = \begin{cases} 0 & \text{if } l < \varepsilon\lambda \\ 1 & \text{if } l \geq \varepsilon\lambda \end{cases}$$

where $0 < \varepsilon < 1$.

The system looks as follows:

$$\begin{cases} \frac{\partial F}{\partial \tau} = \frac{\lambda S(\lambda, \tau)}{1 + \int_{\varepsilon\lambda}^1 S(l, \tau) dl} - F(\lambda, \tau) \\ \frac{\partial S}{\partial \tau} = PF(\lambda, \tau) - C\lambda S(\lambda, \tau) \end{cases} \quad (2.35)$$

Let $H(\lambda, \tau) = 1 + \int_{\varepsilon\lambda}^1 S(l, \tau) dl$.

This means that the system can be rewritten as

$$\begin{cases} \frac{\partial F}{\partial \tau} = -\frac{\lambda}{\varepsilon} \frac{\partial H(\lambda/\varepsilon, \tau)}{\partial \lambda} \frac{1}{H(\lambda, \tau)} - F(\lambda, \tau) \\ -\frac{1}{\varepsilon^2} \frac{\partial^2 H(\lambda/\varepsilon, \tau)}{\partial \lambda^2} = PF(\lambda, \tau) + C \frac{\lambda}{\varepsilon} \frac{\partial H(\lambda/\varepsilon, \tau)}{\partial \lambda} \end{cases} \quad (2.36)$$

Here,

$$S(\varepsilon\lambda, \tau) = -\frac{1}{\varepsilon} \frac{\partial H}{\partial \lambda}. \quad (2.37)$$

$H(\lambda, \tau)$ has several constraints. First, since $S(1, \tau) = 0$ is a boundary condition, this means that

$$H(1/\varepsilon, \tau) = 1. \quad (2.38)$$

Also, since $S(\lambda, \tau)$ must be non-negative on $[0, 1]$,

$$\frac{\partial H}{\partial \lambda} \leq 0 \text{ on } [0, 1/\varepsilon].$$

And if $S(\lambda, \tau)$ must be positive (*e.g.* for a non-zero steady state), then

$$\frac{\partial H}{\partial \lambda} < 0 \text{ on } [0, 1/\varepsilon]. \quad (2.39)$$

2.5.2 Steady states and stability

Let $H(\lambda, \tau) = h(\lambda) + h(\lambda, \tau)$ and $F(\lambda, \tau) = f(\lambda) + f(\lambda, \tau)$ where

$$-\frac{\lambda}{\varepsilon} \frac{\partial h(\lambda/\varepsilon, \tau)}{\partial \lambda} \frac{1}{h} - f = 0 \quad (2.40)$$

and

$$Pf + C \frac{\lambda}{\varepsilon} \frac{\partial h(\lambda/\varepsilon, \tau)}{\partial \lambda} = 0 \quad (2.41)$$

Now (2.20) implies that

$$\frac{\lambda}{\varepsilon} \frac{\partial h(\lambda/\varepsilon, \tau)}{\partial \lambda} = -hf \quad (2.42)$$

Plugging this in into (2.21)

$$Pf - Chf = 0$$

or

$$f(P - Ch) = 0$$

This means that either $f = 0$ or $h = P/C$ or both.

$$\text{If } h = P/C \quad (2.43)$$

then

$$f = -\frac{\lambda}{\varepsilon} \frac{\partial h(\lambda/\varepsilon, \tau)}{\partial \lambda} \frac{1}{h}$$

$$= -\frac{\lambda}{\varepsilon} \frac{\partial \left(\frac{P}{C}(\lambda/\varepsilon) \right)}{\partial \lambda} \frac{C}{P}. \quad (2.44)$$

Also from (2.38) and (2.39) $\frac{P}{C}(1/\varepsilon) = 1$ and $\frac{\partial(P/C)}{\partial \lambda} < 0$ on $[0, 1/\varepsilon]$.

Boundary conditions also imply that since $\frac{\partial h(1/\varepsilon)}{\partial \lambda} = 0$, $\frac{\partial(P/C)(1/\varepsilon)}{\partial \lambda} = 0$.

If $f = 0$ then (2.22) implies that $\frac{\partial h}{\partial \lambda} = 0$, *i.e.* $h = h_0$ where h_0 is a constant. Since a steady state with a seedbank and no flowers is not possible, h_0 is set to 1, which corresponds to $s_0 = 0$, *i.e.* extinction of seeds and flowers.

Note that if $\frac{P}{C}$ is a constant, then $\frac{\partial(P/C)}{\partial \lambda} = 0$, and therefore $f=0$.

Therefore, steady states are

$$(f, h) \quad \text{and} \quad (0, h_0).$$

Again, it was not possible to complete a full stability analysis for this system and this is the subject of further work. Consequently, numerical simulation were performed.

2.5.3 Numerical simulation results

The results for the stability of the $(f, s)=(0, 0)$ steady state were similar to the results for the model in Section 2.2.2. The simulations revealed that the $(0, 0)$ steady state is a stable node if $\frac{P}{C}(\lambda) < 1$. Simulations were performed with $\frac{P}{C}(\lambda) < 1$: case 1) $P=0.2$, and $C=0.5$; case 2) $P=4\lambda^2$ and $C=0.5$. Two sets of initial conditions were used: 1) $(F(\lambda), S(\lambda)) = (1, 1)$ and 2) $F(\lambda)$ and $S(\lambda)$ picked randomly from the range $(0, 100)$. In all simulations, the system immediately settled to the $(0, 0)$ state.

To investigate the stability of the non-zero steady state, two functions of $P(\lambda)$ were used for simulations:

Case 1: $P(\lambda) = (\lambda - 2)^2 + 2.5$ and $C=1.5$.

If $\varepsilon=0.5$, then substituting for $\frac{P}{C}(\lambda)$ in (2.37) and (2.43),

$$s(\lambda) = \frac{32}{3}(1 - \lambda),$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.44)

$$f(\lambda) = 16 \frac{\lambda - \lambda^2}{(\lambda - 2)^2 + 2.5}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing

on the interval (0,1), and $\frac{P}{C}(1) - 1 = \frac{4}{3}$ is positive.

Case 2: $P(\lambda) = \frac{1}{4\lambda - \lambda^2 + 1} + 2$ and $C=1.5$.

If $\varepsilon = 0.5$, then substituting for $\frac{P}{C}(\lambda)$ in (2.37) and (2.43),

$$s(\lambda) = \frac{8}{3} \frac{(2 - \lambda)}{(4\lambda - \lambda^2 + 1)^2},$$

and substituting for $\frac{P}{C}(\lambda)$ in (2.44),

$$f(\lambda) = 4 \frac{2\lambda - \lambda^2}{(4\lambda - \lambda^2 + 1)^2 \left(\frac{1}{4\lambda - \lambda^2 + 1} + 2 \right)}.$$

$\frac{P}{C}(\lambda)$ satisfies the conditions for the existence of the non-zero state, *i.e.* it is decreasing

on the interval (0,1), and $\frac{P}{C}(1) - 1 = \frac{3}{4}$ is positive.

Simulations were performed with three different initial conditions: the steady state, $F(\lambda)$ and $S(\lambda)$ set to 1 for all λ , and $F(\lambda)$ and $S(\lambda)$ assigned a random value between 0 and 100 (not including endpoints).

When the equation solver was used to confirm the analysis, the predicted steady state was not stable in both cases. In fact, instabilities appeared, and eventually (on the order of 5,000 time steps) the system evolved to a discrete state. Figure 2.8 shows

examples of the case 1 with initial conditions set to the steady state, developing instabilities and the stable state of a run with $\varepsilon=0.5$. It was not possible to conduct a complete stability analysis and therefore, at present, the origin of the peaks is not clear. However, there is an important difference in the way that the integral is calculated in the case of $\varepsilon \neq 1$, which leads to an unavoidable error. The competition integral was calculated on the interval $[\varepsilon\lambda, 1)$. When $\varepsilon\lambda$ is calculated, the discretisation leads to the integral for different values of λ to be the same (which should not occur). For example, for $\varepsilon=0.5$ and $\lambda=0.99$ and λ -step of 0.01 the integral should be calculated on the interval $[0.495, 1)$. However, since the λ -step is 0.01, 0.0495 is rounded to 0.49. Now, for $\lambda=0.98$, the interval is also $[0.49, 1)$. Refining the discretisation, *i.e.* letting λ -step to be smaller, did not eliminate the peaks, but changed the time at which the instability developed. This was tested for λ -step of 0.1 and 0.002. In case with λ -step 0.1 the discrete state evolved after approximately 1,000 steps, and if λ -step was set to 0.005, the discrete state evolved after approximately 20,000 steps. The change in the resolution of the integration did not affect the location of the peaks and the final state was identical.

The error in the competition integral led to instabilities. However, this 'error' may have its origins in a more realistic representation of the ecosystem. Since, in reality, any ecosystem has a finite number of individuals, the space of λ is occupied at discrete points, with S and F discrete functions. This case is discussed in the following section.

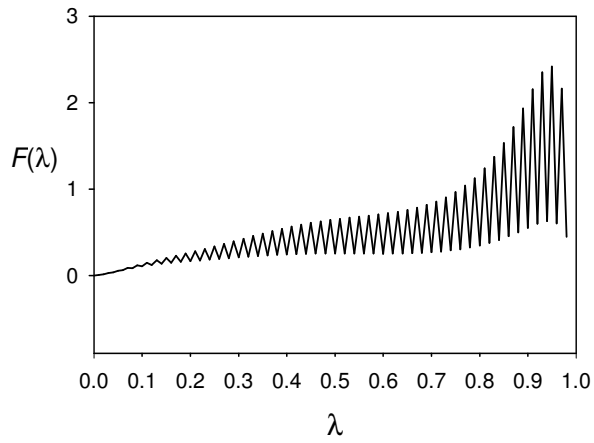


Fig. 2.8 a) time step 300;

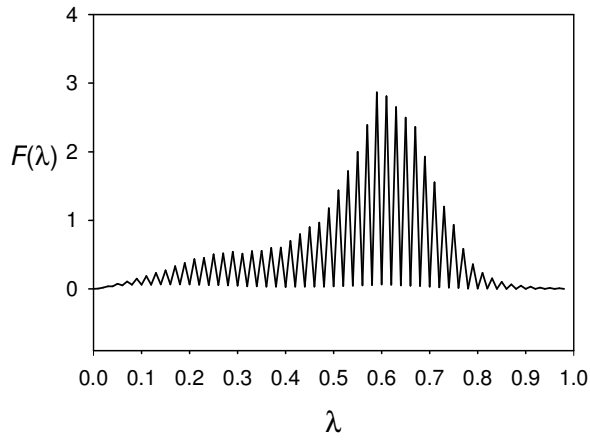


Fig. 2.8 b) time step 1,000;

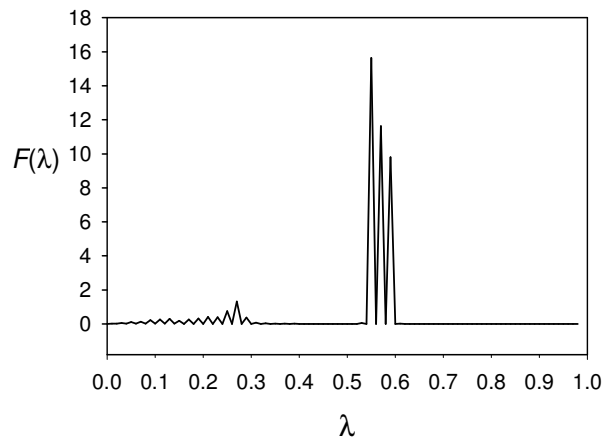


Fig. 2.8 c) time step 3,000;

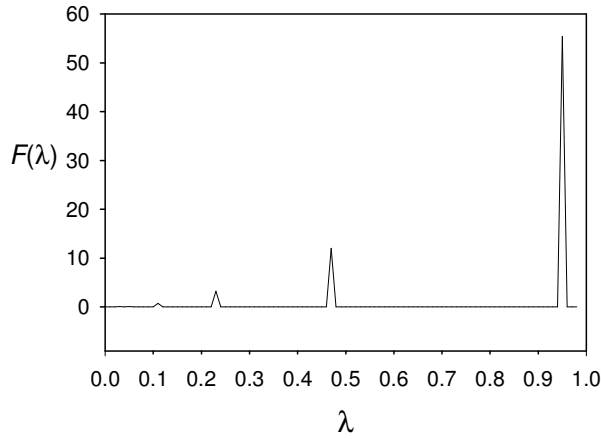


Fig. 2.8 d) the final distribution of the number of adult individuals $F(\lambda)$ across λ values at time step 36,000.

Figure 2.8 An example of numerical simulation results. The distribution of the number of adults $F(\lambda)$ for $\lambda=0.5$. The plots a) to d) show development of peaks starting from the steady state predicted by analysis.

2.6 The discrete version of the model

2.6.1 Model definition

Instead of the continuous functions F and S , consider a set of n discrete values (F_i, S_i) for each $\lambda_i, i=1, \dots, n$, with λ_i in the range $[0,1)$. The system (2.35) becomes:

$$\begin{cases} \frac{dF_i}{d\tau} = \frac{\lambda_i S_i(\tau)}{1 + (\Delta\lambda) \sum_{j=i-k}^n S_j(\tau)} - F_i(\tau) \\ \frac{dS_i}{d\tau} = P_i F_i(\tau) - C \lambda_i S_i(\tau) \end{cases}$$

where $\Delta\lambda$ is the difference between λ_i and λ_{i+1} , and k is a number such that $i-k=\varepsilon i$.

2.6.2 A simple model of two competing populations

First, consider a simple system of two populations (F_1, S_1) and (F_2, S_2) , which affect each other through competition, with values λ_1 and λ_2 . The system is the following

$$\begin{cases} \frac{dF_1}{d\tau} = \frac{\lambda_1 S_1(\tau)}{1 + (\Delta\lambda)(S_1(\tau) + S_2(\tau))} - F_1(\tau) = g_1(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \frac{dS_1}{d\tau} = P_1 F_1(\tau) - C \lambda_1 S_1(\tau) = h_1(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \frac{dF_2}{d\tau} = \frac{\lambda_2 S_2(\tau)}{1 + (\Delta\lambda)(S_1(\tau) + S_2(\tau))} - F_2(\tau) = g_2(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \\ \frac{dS_2}{d\tau} = P_2 F_2(\tau) - C \lambda_2 S_2(\tau) = h_2(F_1(\tau), S_1(\tau), F_2(\tau), S_2(\tau)) \end{cases}$$

Let f_1, s_1, f_2 and s_2 be the steady state solutions. Then, the possible steady states for this system are:

$$\begin{aligned} \{f_1, s_1, f_2, s_2\} &= \{0, 0, 0, 0\}; \\ &= \{f_1, s_1, 0, 0\} \text{ where } f_1 \neq 0, s_1 \neq 0; \\ &= \{0, 0, f_2, s_2\} \text{ where } f_2 \neq 0, s_2 \neq 0; \\ &= \{f_1, s_1, f_2, s_2\} \text{ where } f_i \neq 0, s_i \neq 0, i = 1, 2; \end{aligned}$$

For the case $\{f_1, s_1, 0, 0\}$ (where $f_1 \neq 0, s_1 \neq 0$), the steady state is:

$$\begin{cases} 0 = \frac{\lambda_1 s_1}{1 + (\Delta\lambda)(s_1)} - f_1 \\ 0 = P_1 f_1 - C \lambda_1 s_1 \end{cases}$$

This implies that

$$\frac{1}{1 + (\Delta\lambda)s_1} = \frac{f_1}{\lambda_1 s_1} = \frac{C \lambda_1 s_1}{P_1 \lambda_1 s_1} = \frac{C}{P_1} \quad (2.45)$$

and therefore,

$$s_1 = \frac{1}{(\Delta\lambda)} \left(\frac{P_1}{C} - 1 \right)$$

and

$$f_1 = \frac{C \lambda_1 s_1}{P_1} = \frac{1}{(\Delta\lambda)} \frac{\lambda_1 (P_1 - C)}{P_1}.$$

Similarly, for the steady state $\{0, 0, f_2, s_2\}$ (where $f_2 \neq 0, s_2 \neq 0$)

$$s_2 = \frac{1}{(\Delta\lambda)} \left(\frac{P_2}{C} - 1 \right)$$

and

$$f_2 = \frac{C \lambda_2 s_2}{P_2} = \frac{1}{(\Delta\lambda)} \frac{\lambda_2 (P_2 - C)}{P_2}.$$

For the steady state $\{f_1, s_1, f_2, s_2\}$ (where $f_i \neq 0, s_i \neq 0, i = 1, 2$),

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_1}{C}, \quad (2.46)$$

and

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_2}{C} \quad (2.47)$$

are required for existence of the steady state. This is not possible unless $P_1 = P_2$. Assume that $P_1 = P_2 = P_0$. In that case both populations coexist, and their values are determined by the initial conditions and by the relationship

$$1 + (\Delta\lambda)(s_1 + s_2) = \frac{P_0}{C}, \quad (2.48)$$

and therefore

$$s_1 + s_2 = \frac{1}{(\Delta\lambda)} \left(\frac{P_0}{C} - 1 \right).$$

This is the only constraint, and having picked the values of s_1 and s_2 , f_1 and f_2 can be found by

$$f_i = \frac{C\lambda_i s_i}{P_0} \text{ for } i=1,2.$$

Linear stability analysis (Appendix A.3) suggests that the zero state is stable if either

- a) $P_1 > C$ and $P_2 > C$ or
- b) $P_1 < C$ and $P_2 < C$.

Case a) implies that either $C < P_1 < P_2$ or $C < P_2 < P_1$.

Case b) implies that either $P_1 < P_2 < C$ or $P_2 < P_1 < C$.

For the steady state $\{f_1, s_1, 0, 0\}$ (where $f_1 \neq 0, s_1 \neq 0$), linear stability analysis suggests that either

- a) $P_1 > C$ and $P_1 > P_2$ or
- b) $P_1 < C$ and $P_1 < P_2$.

Case a) implies that either $C < P_2 < P_1$ or $P_2 < C < P_1$.

Case b) implies that either $P_1 < P_2 < C$ or $P_1 < C < P_2$.

Similarly, for the case $\{0, 0, f_2, s_2\}$ (where $f_2 \neq 0, s_2 \neq 0$), the state is stable if either

a) $P_2 > C$ and $P_2 > P_1$, *i.e.* $C < P_1 < P_2$ or $P_1 < C < P_2$ or

b) $P_2 < C$ and $P_2 < P_1$, *i.e.* $P_2 < P_1 < C$ or $P_2 < C < P_1$.

Notice that if

$$C < P_1 < P_2 \text{ or } P_2 < P_1 < C,$$

then both the zero-state and $\{0, 0, f_2, s_2\}$ are stable, and

if $C < P_2 < P_1$ or $P_1 < P_2 < C$,

then both the zero-state and $\{f_1, s_1, 0, 0\}$ are stable.

For the steady state $\{f_1, s_1, f_2, s_2\}$ (where $f_i \neq 0, s_i \neq 0, i = 1, 2$), and $P_1 = P_2 = P_0$, linear stability analysis gives zero for $\det M$. Hence, it does not provide information about stability in this case.

These are the results when individuals have one or two values of the parameter λ . This situation can be extended to more than two values (Appendix B).

2.6.3 Simulation results for a system of two populations

Simulations with two populations were performed, *i.e.* the populations with different values of λ were set to zero for all values of λ but two (with both affecting each other through competition). In that case, as the analysis predicted, population with only one value of λ survived if the values of P were different for the two populations. The simulations also showed that the population with a higher P value was the one that always survived. If the value of P was the same for the two populations, the system settled to the nearest point satisfying (2.48). Simulations with three and seven populations were performed as well, with the same results.

2.6.4 Effects of outside competition on a system with two populations

Now, extend the two population model to any two populations with reproduction rates λ_k and λ_{k-1} with $\lambda_k > \lambda_{k-1}$ for which the competition term, *i.e.* the sum of populations contributing to the competition, is the same. This occurs if $\lambda_{k-1} \subset (\varepsilon \lambda_k, 1)$. Now, suppose there are two populations with λ_k and λ_{k-1} , and the competition term is the same for the two, and $P_k = P_{k-1} = P_0$.

$$\left\{ \begin{array}{l} \frac{dF_k}{d\tau} = \frac{\lambda_k S_k}{1 + (\Delta\lambda)(S_k + S_{k-1} + \sum_{j=k+1}^n S_j)} - F_k \\ \frac{dS_k}{d\tau} = P_k F_k - C \lambda_k S_k \\ \frac{dF_{k-1}}{d\tau} = \frac{\lambda_{k-1} S_{k-1}}{1 + (\Delta\lambda)(S_k + S_{k-1} + \sum_{j=k+1}^n S_j)} - F_{k-1} \\ \frac{dS_{k-1}}{d\tau} = P_{k-1} F_{k-1} - C \lambda_{k-1} S_{k-1} \end{array} \right.$$

Let $(s_k, f_k, s_{k-1}, f_{k-1})$ be the non-zero steady state. It exists if

$$1 + (\Delta\lambda)(s_k + s_{k-1} + \sum_{j=k+1}^n s_j) = \frac{P_0}{C},$$

i.e.

$$s_k + s_{k-1} = \frac{1}{(\Delta\lambda)} \left[\frac{P_0}{C} - 1 \right] - \sum_{j=k+1}^n s_j.$$

Those s_i in the sum that have the same competition term (the sum of other s values with which s_i competes), call it T_j , can be grouped together. Suppose there are l such groups, and therefore $j=1, \dots, l$. Then, in the steady state

$$\sum_{j=k+1}^n s_j = \underbrace{\sum_{j=k+1}^{m_1} s_j}_{T_1, P_1} + \underbrace{\sum_{j=m_1+1}^{m_2} s_j}_{T_2, P_2} + \dots + \underbrace{\sum_{j=m_{l-1}+1}^n s_j}_{T_l, P_l}$$

In order that s_j within each group can coexist, it is necessary that

$$1 + (\Delta\lambda) \sum_{j=m_i+1}^{m_{i+1}} s_j = \frac{P_i}{C} \Rightarrow \sum_{j=m_i+1}^{m_{i+1}} s_j = \frac{1}{(\Delta\lambda)} \left[\frac{P_i}{C} - 1 \right],$$

for any $i=1, \dots, l$.

This means that

$$\sum_{j=k+1}^n s_j = \frac{1}{(\Delta\lambda)} \left[\frac{P_1}{C} - 1 + \frac{P_2}{C} - 1 + \dots + \frac{P_l}{C} - 1 \right]$$

and

$$s_k + s_{k-1} = \frac{1}{(\Delta\lambda)} \left[\left(\frac{P_0}{C} - 1 \right) - \left(\frac{P_1 + P_2 + \dots + P_l}{C} - l \right) \right].$$

Thus, s_k and s_{k-1} can assume any combination of values satisfying the above equality.

For $s_k + s_{k-1}$ to be positive,

$$\frac{P_0}{C} - 1 > \frac{P_1 + P_2 + \dots + P_l}{C} - l,$$

and therefore

$$P_0 > P_1 + \dots + P_l - C(l-1).$$

This condition means that P_i has to be a decreasing step function of λ , where each step is an interval of λ values on which the corresponding values of s_i have the same competition term.

2.6.5 Simulation results for a system of two populations with outside competition

Simulations were performed using a monotonically decreasing function for $P(\lambda)$ and constant C . This form of $P(\lambda)$ is one of the conditions for the existence of the non-zero steady state in the continuous case. The simulations were started in the non-zero steady state predicted by the analysis. The system did not remain in the 'steady' state, but instead developed instabilities and evolved to a function consisting of discrete peaks (as seen on Figure 2.8 d). The sequence of λ positions (from 0 through 0.99) at which populations remained was: 0, 0.02, 0.06, 0.14, 0.30, 0.62 ($\Delta\lambda$ was 0.01).

The separation of the λ positions can be explained from the considerations outlined in sections 2.6.2 and 2.6.4. Since $P(\lambda)$ is monotonically decreasing,

- a) only one population for the interval with the same competitive term (call the interval I_i) can survive;
- b) the highest value of $P(\lambda)$ will be the first population at I_i (since $P(\lambda)$ is monotonically decreasing).

For convenience refer to the positions of λ as 0 through 99 (with 99 corresponding to 0.99).

Look at the intervals I_i :

$I_1=[0,1]$: $s(\lambda)$ at 0 is has the highest $P(\lambda)$, so there is a population at 0.

$I_2=[1,2,3]$: $s(\lambda)$ at 1 cannot survive, so $s(\lambda)$ at 2 survives, so $s(\lambda)$ at 3 does not.

$I_3=[2,3,4,5]$: $s(\lambda)$ at 2 survives, so $s(\lambda)$ at 3-5 do not.

$I_4=[3-7]$: $s(\lambda)$ at 3 to 5 does not survive, so $s(\lambda)$ at 6 survives and so $s(\lambda)$ at 7 does not.

$I_5=[4-9]$: $s(\lambda)$ at 6 survives, others do not.

$I_6=[5-11]$: $s(\lambda)$ at 6 survives, others do not.

$I_7=[6-13] : s(\lambda)$ at 6 survives, others do not.

$I_8=[7-14] : s(\lambda)$ at 14 survives, since all previous do not.

etc...

This scheme produces exactly the spacing of λ resulting in the simulations.

This spacing of populations is

- a) independent of the particular shape of $P(\lambda)$, given that it is monotonic decreasing;
- b) the λ values for which populations survive depend on the λ step, not on the populations' relative positions in the $[0,1)$ interval.

This scenario is a sequential phenomenon, *i.e.* the outcome at the interval depends on the outcome at the previous interval with lower values of λ . One question regarding this scenario is whether some populations, at λ positions that are predicted to survive, go extinct before the final spacing is reached. In fact, the simulation shows that populations that are predicted to survive can reach very small values (order of magnitude 10^{-7}), but then recover. In real communities, the populations cannot persist at such levels, and will go extinct. This may affect the persistence of individuals with other values of λ .

2.7 Discrete vs. continuous – individuals vs. populations

Analysis of the continuous and the discrete version of the model revealed some

interesting differences between the two. The general requirement for $\frac{P}{C}(\lambda)$ to be a

decreasing function was observed in both cases. However, in the continuous case,

$\frac{P}{C}(\lambda)$ had to be monotonic decreasing, whereas this condition was weakened in the

discrete case and $\frac{P}{C}(\lambda)$ could be a non-increasing step function. Moreover,

simulations revealed that the dynamics of the model in the discrete case lead to a

steady state consisting of peaks spaced in the manner described above. The difference

between the discrete and the continuous models suggests that discreteness resulting

from finite populations may play an important role in shaping the relative abundance

of individuals across a range of trait values.

2.8 Lessons learned: the role of individuals

The results of the model show a link between physiological traits of individuals and community diversity.

- A trade-off between physiological traits of individuals in the model determined the existence of diversity in the community. Moreover, it determined the relative abundance of individuals across the range of trait values. This gives an indication that individual traits may play an important role in shaping the diversity in the community. The form of the genetic coupling had the same effects on the community.

Discrete and continuous models, while similar in the general conclusion, differed in the steady-state shape of the population distribution along the range of trait values. The simulations of the discrete model consistently produced a steady state distribution with populations located at precise values of the growth rate λ (Figure 2.8 c)). The intervals of separation depended on the description of competition.

- These results show that considering finite populations can have an important impact on the community dynamics. It is crucial to explore this impact, since biological communities are always discrete in this sense.
- The results also suggested that the nature of competition between individuals in a community may also be important in determining the resulting steady state.