

## Introduction to Theoretical Ecology (EEB5096)

### Final exam (2022/1/11)

1. In this course, we have learned multiple models that aim to describe the dynamics of a predator-prey system, some of which produce cyclic dynamics while others produce stable point equilibrium. Consider the following model where the prey species,  $N(t)$ , grows exponentially and the predator species,  $P(t)$ , consumes prey via type-II functional response:

$$\frac{dN}{dt} = rN - \left( \frac{aN}{1 + ahN} \right) P$$

$$\frac{dP}{dt} = e \left( \frac{aN}{1 + ahN} \right) P - dP$$

Here,  $r$  is the intrinsic growth rate of the prey,  $a$  is the consumption efficiency of the predator,  $h$  is handling time of the predator;  $e$  and  $d$  are the assimilation efficiency and the mortality rate of the predator, respectively. We assume  $e > dh$  for feasibility.

- (1) Use the ZNGIs to find all (non-negative) equilibrium points of this model. [5 pts]
- (2) Draw the ZNGI on the state-space and use the graphical method to predict the stability of those equilibrium. [5 pts]
- (3) Use local stability analysis to determine the stability of those equilibrium. [10 pts]

### Solution

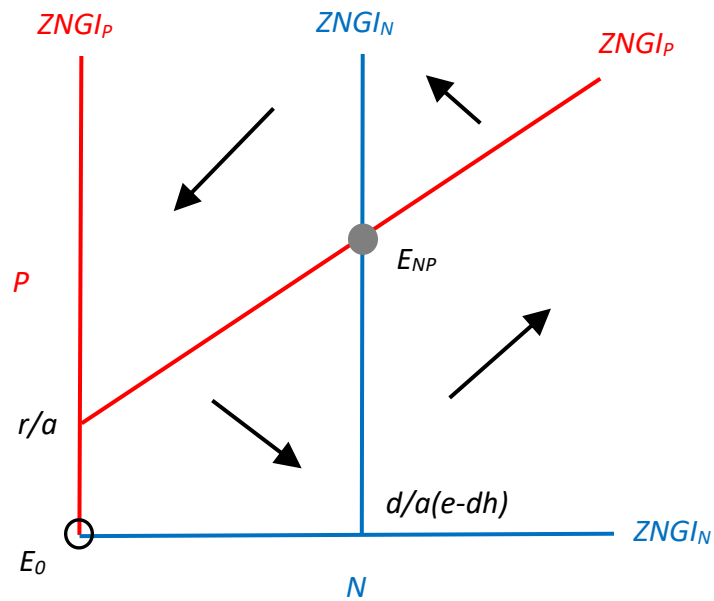
(1)

$$\frac{dN}{dt} = N \left( r - \frac{aP}{1 + ahN} \right) = 0 \rightarrow N^* = 0 \text{ or } P^* = \frac{r}{a} (1 + ahN^*)$$

$$\frac{dP}{dt} = P \left( \frac{eaN}{1 + ahN} - d \right) = 0 \rightarrow P^* = 0 \text{ or } N^* = \frac{d}{a(e - dh)}$$

→ The equilibrium points are  $E_0 = (0, 0)$  and  $E_{NP} = \left( \frac{d}{a(e - dh)}, \frac{r(1 + \frac{dh}{e - dh})}{a} \right)$

(2)



$E_0$  is unstable;  $E_{NP}$  is undetermined (spiral)

(3)

The Jacobian of the system is:

$$J = \begin{bmatrix} r - \frac{a}{(1+ahN)}P + \frac{a^2hNP}{(1+ahN)^2} & -\frac{aN}{1+ahN} \\ \frac{eaP}{(1+ahN)^2} & \frac{eaN}{1+ahN} - d \end{bmatrix}$$

a.  $E_0 = (0, 0)$ :

- $J_{E_0} = \begin{bmatrix} r & 0 \\ 0 & -d \end{bmatrix}$
- Eigenvalues:  $r, -d$
- Unstable

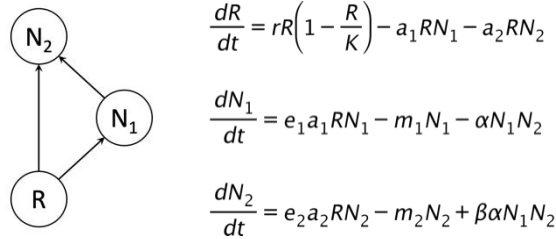
b.  $E_{NP} = \left( \frac{d}{a(e-dh)}, \frac{r(1+\frac{dh}{(e-dh)})}{a} \right)$ :

•  $J_{E_{NP}} = \begin{bmatrix} \frac{a^2 h N P}{(1+ahN)^2} & -\frac{aN^*}{1+ahN^*} \\ \frac{eaP^*}{(1+ahN^*)^2} & 0 \end{bmatrix}$

• Characteristic equation:  $\lambda^2 - \frac{a^2 h N P}{(1+ahN)^2} \lambda + \frac{ea^2 N^* P^*}{(1+ahN^*)^3} = 0$

•  $\lambda_1 + \lambda_2 = \frac{a^2 h N P}{(1+ahN)^2} > 0 \rightarrow \text{Unstable}$

2. Intraguild predation (IGP) describes the trophic module with omnivorous interactions among consumers. Consider two consumers ( $N_1(t)$  and  $N_2(t)$ ) both consuming one logistically-growing resource ( $R(t)$ ). Moreover,  $N_1$  (the IG-prey) is also consumed by  $N_2$  (the IG-predator). All trophic interactions follow type-I functional response. The system is as follows:



$$\frac{dR}{dt} = rR \left( 1 - \frac{R}{K} \right) - a_1 R N_1 - a_2 R N_2$$

$$\frac{dN_1}{dt} = e_1 a_1 R N_1 - m_1 N_1 - \alpha N_1 N_2$$

$$\frac{dN_2}{dt} = e_2 a_2 R N_2 - m_2 N_2 + \beta \alpha N_1 N_2$$

Here,  $r$  and  $K$  are the intrinsic growth rate and carrying capacity of the resource, respectively. For the two consumers,  $a_i$  ( $i = 1$  or  $2$ ) are the consumption efficiencies,  $e_i$  are the assimilation efficiencies, and  $m_i$  are the mortality rates. The parameter  $\alpha$  and  $\beta$  capture the consumption and assimilation efficiencies of intraguild predation between  $N_1$  and  $N_2$ .

- (1) The  $R^*$  value (i.e., the resource value that results in zero growth when consumer are growing in monoculture) for  $N_1$  and  $N_2$  is  $m_1/(e_1 a_1)$  and  $m_2/(e_2 a_2)$ , call them  $R_1^*$  and  $R_2^*$ , respectively. In your opinion, if we want the three species to coexist in the presence of IGP, which one of  $R_1^*$  and  $R_2^*$  should be larger, why? [2.5 pts]
- (2) Write out the invasion criteria for the IG-prey (into the equilibrium system with  $N_2$  &  $R$ ) and the IG-predator (into the equilibrium system with  $N_1$  &  $R$ ). [10 pts]

- (3) Rearrange the above invasion criteria and let  $R_1^*$  and  $R_2^*$  show up in the express. Based on question (1), discuss how the difference between  $R_1^*$  and  $R_2^*$ , and the strength of IGP ( $\alpha$  and  $\beta$ ) affect a species' ability to invade the monoculture equilibrium of the other species. [5 pts]
- (4) In this system, mutual invasion (and therefore coexistence) is possible. Assume that the parameters produce a feasible coexistence equilibrium (i.e.,  $E_c(R^* > 0, N_1^* > 0, N_2^* > 0)$ ), write out the jacobian matrix and its characteristic equation in terms of  $R^*$ ,  $N_1^*$ , and  $N_2^*$  (i.e., you do not need to show the actual full expression of this coexistence equilibrium). [7.5 pts]
- (5) Applying the Routh-Hurwitz criterion to the above characteristic equation, unfortunately, is quite tedious (so I'll spare you from that!). The take home message is that despite mutual invasibility and feasibility, the coexistence equilibrium is not always stable. Simulate the below two sets of parameters (with initial condition  $N_1(0) = N_2(0) = 0.01, R(0) = 0.5$ ) and tell me what dynamics you see. [5 pts]
- $a_1 = 1.0, a_2 = 0.3, e_1 = 1.0, e_2 = 0.3, m_1 = m_2 = 0.5, \alpha = 0.5, \beta = 1.0, r = 1.0, K = 10.0$
  - $a_1 = 1.0, a_2 = 0.3, e_1 = 1.0, e_2 = 0.3, m_1 = m_2 = 0.5, \alpha = 0.5, \beta = 1.0, r = 1.0, K = 25.0$

### Solution

(1)

$R_2^*$  should be greater than  $R_1^*$  for  $N_1$  (IG prey) and  $N_2$  (IG predator) to coexist. This is because  $N_1$  benefits  $N_2$  while  $N_2$  negatively affects  $N_1$ , and therefore if  $R_1^* > R_2^*$ , then  $N_1$  will not be able to survive as it suffers two disadvantages.

(2)

- The invasion criterion for  $N_1$  at  $N_2$  monoculture equilibrium  $(R_2^*, N_2^*) =$

$(\frac{m_2}{e_2 a_2}, \frac{r(1 - \frac{m_2}{e_2 a_2 K})}{a_2})$  is:

$$\lim_{N_1 \rightarrow 0} \frac{1}{N_1} \frac{dN_1}{dt} \Big|_{R=R_2^*, N_2=N_2^*} = e_1 a_1 \frac{m_2}{e_2 a_2} - m_1 - \frac{\alpha r (1 - \frac{m_2}{e_2 a_2 K})}{a_2} > 0$$

- The invasion criterion for  $N_2$  at  $N_1$  monoculture equilibrium  $(R_1^*, N_1^*) =$

$(\frac{m_1}{e_1 a_1}, \frac{r(1 - \frac{m_1}{e_1 a_1 K})}{a_1})$  is:

$$\lim_{N_2 \rightarrow 0} \frac{1}{N_2} \frac{dN_2}{dt} \big|_{R=R_1^*, N_1=N_1^*} = e_2 a_2 \frac{m_1}{e_1 a_1} - m_2 + \frac{\beta \alpha r (1 - \frac{m_1}{e_1 a_1 K})}{a_1} > 0$$

(3)

Rearrange the invasion growth equations in (2), we get:

$$IGR_{N_1} = e_1 a_1 \left( \frac{m_2}{e_2 a_2} - \frac{m_1}{e_1 a_1} \right) - \frac{\alpha r (1 - \frac{m_2}{e_2 a_2 K})}{a_2} = e_1 a_1 (R_2^* - R_1^*) - \frac{\alpha r (1 - \frac{R_2^*}{K})}{a_2}$$

$$IGR_{N_2} = e_2 a_2 \left( \frac{m_1}{e_1 a_1} - \frac{m_2}{e_2 a_2} \right) + \frac{\beta \alpha r (1 - \frac{m_1}{e_1 a_1 K})}{a_1} = -e_2 a_2 (R_2^* - R_1^*) + \frac{\beta \alpha r (1 - \frac{R_1^*}{K})}{a_1}$$

→ Larger difference between  $R_2^*$  and  $R_1^*$  (i. e.,  $R_2^* - R_1^*$ ) as well as lower consumption rate  $\alpha$  promote the invasion of  $N_1$  into  $N_2$  monoculture equilibrium

→ Smaller difference between  $R_2^*$  and  $R_1^*$  (i. e.,  $R_2^* - R_1^*$ ), higher consumption rate  $\alpha$ , and higher assimilation efficiency  $\beta$  promote the invasion of  $N_2$  into  $N_1$  monoculture equilibrium

(4)

The Jacobian evaluated at the internal equilibrium  $E_c$  :

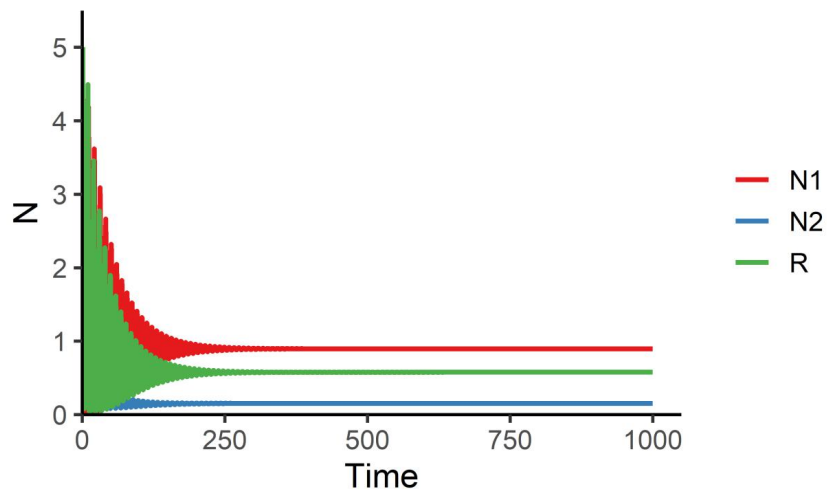
$$J_{E_c} = \begin{bmatrix} (-\frac{r}{K})R^* & -a_1 R^* & -a_2 R^* \\ e_1 a_1 N_1^* & 0 & -\alpha N_1^* \\ e_2 a_2 N_2^* & \beta \alpha N_2^* & 0 \end{bmatrix}$$

- Characteristic equation:

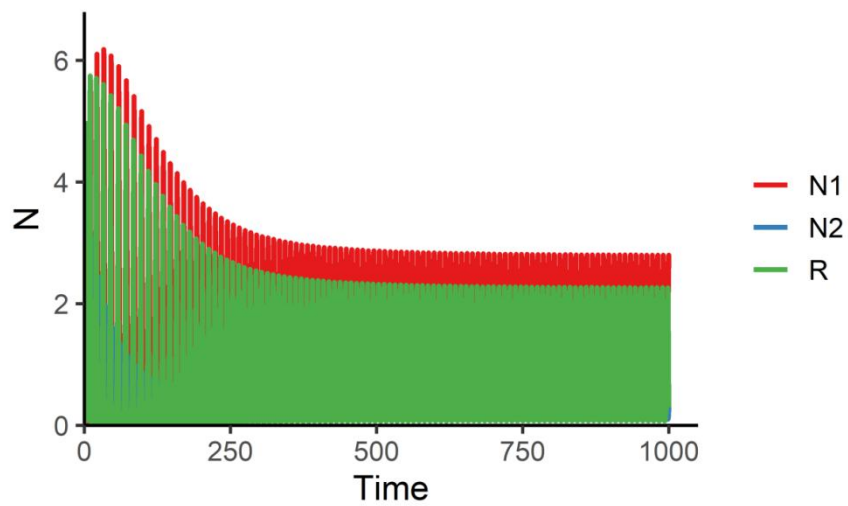
$$\lambda^3 + \left(\frac{r}{K}R^*\right)\lambda^2 + (\alpha^2\beta N_1^*N_2^* + a_1^2e_1R^*N_1^* + a_2^2e_2R^*N_2^*)\lambda + \left(\frac{r\alpha^2\beta}{K}R^*N_1^*N_2^* - a_1a_2e_2\alpha R^*N_1^*N_2^* + a_1a_2e_1\alpha\beta R^*N_1^*N_2^*\right) = 0$$

(5)

- Parameter set 1:  $R$ ,  $N_1$ , and  $N_2$  stably coexist



- Parameter set 2:  $R$ ,  $N_1$ , and  $N_2$  exhibit stable limit cycles



## R code

```
library(tidyverse)
library(deSolve)

IGP_model_fun <- function(a1, a2, e1, e2, m1, m2, alpha, beta, r, K) {

  IGP_model <- function(times, state, parms){
    with(as.list(c(state, parms)), {
      dR_dt = r*R*(1-R/K)-a1*R*N1-a2*R*N2
      dN1_dt = e1*a1*R*N1-m1*N1-alpha*N1*N2
      dN2_dt = e2*a2*R*N2-m2*N2+beta*alpha*N1*N2

      return(list(c(dR_dt, dN1_dt, dN2_dt)))
    })
  }

  times <- seq(1, 1000, by = 0.1)
  parms <- c(a1 = a1, a2 = a2, e1 = e1, e2 = e2,
            m1 = m1, m2 = m2, alpha = alpha, beta = beta,
            r = r, K = K)
  state <- c(R = 5, N1 = 2, N2 = 1)

  pop_size <- ode(func = IGP_model, times = times, y = state, parms = parms)

  pop_size %>%
    as.data.frame() %>%
    pivot_longer(cols = -time, names_to = "species", values_to = "N") %>%
```

```

ggplot(aes(x = time, y = N, color = species)) +
  geom_line(size = 1) +
  theme_classic(base_size = 14) +
  labs(x = "Time", y = "N") +
  scale_x_continuous(limits = c(0, 1050), expand = c(0, 0)) +
  scale_y_continuous(limits = c(0, max(pop_size[, -1])*1.1), expand = c(0,
0)) +
  scale_color_brewer(name = NULL, palette = "Set1")
}

```

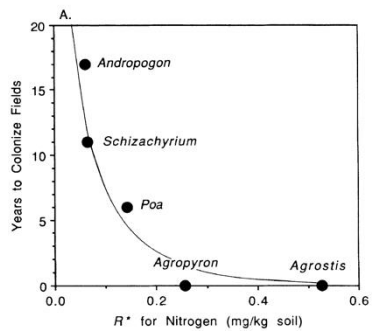
```

IGP_model_fun(a1 = 1.0, a2 = 0.3, e1 = 1.0, e2 = 0.3,
              m1 = 0.5, m2 = 0.5, alpha = 0.5, beta = 1.0,
              r = 1.0, K = 10.0)
IGP_model_fun(a1 = 1.0, a2 = 0.3, e1 = 1.0, e2 = 0.3,
              m1 = 0.5, m2 = 0.5, alpha = 0.5, beta = 1.0,
              r = 1.0, K = 25.0)

```



3. In non-spatial equilibrium models, two competitors cannot coexist on a single limiting resources, known as the  $R^*$  rule. However, in spatially-implicit models, such as those built with a patch occupancy framework, coexistence of multiple species is possible as “space” (i.e., open patches) acts as an additional resource. Coexistence occurs because species with sufficiently high dispersal rates persist in sites that are not yet occupied by superior competitors. That is, a competition-colonization tradeoff (*sensu* Tilman 1994, *Ecology*; see below figure) potentially allows species coexistence. In this question set, we will see how this mechanism works.



The observed interspecific trade-off between the years required for a dominant grass species to invade old fields and the competitive ability of the species for soil nitrogen. Competitive ability is expressed as the  $R^*$  of each species for soil nitrogen, as determined in long-term monocultures of each species on a low nitrogen soil (Tilman 1994, *Ecology*).

- (1) Consider a patch occupancy model tracking the occupancy percentage of species 1,  $P_1(t)$ , with parameters  $c_1$  and  $m$  representing species 1's colonization ability and mortality rate due to disturbance ( $c_1 > m$ ), respectively. Show that in the following equation, at equilibrium, species 1 can never completely fill the habitat unless it is immortal ( $m = 0$ ) or have infinite colonization rate ( $c_1 \rightarrow \infty$ ), both of which are biologically unrealistic. [2.5 pts]

$$\frac{dP_1}{dt} = c_1 P_1 (1 - P_1) - m P_1$$

- (2) Because species 1 cannot occupy all the sites in a habitat, a species that is an inferior competitor (species 2, with occupancy  $P_2(t)$ ) may be able to survive in the open portion of a habitat. Assume that the interactions among the two species are structured to give a strong competitive hierarchy, i.e., species 1 always immediately displaces species 2 when it arrives at a pre-occupied sites of species 2. On the other hand, species 2 can neither invade into nor displace species 1 from a site. This leads to two equations:

$$\begin{aligned}\frac{dP_1}{dt} &= c_1 P_1 (1 - P_1 - P_2) - m P_1 + c_1 P_1 P_2 \\ &= c_1 P_1 (1 - P_1) - m P_1\end{aligned}$$

$$\frac{dP_2}{dt} = c_2 P_2 (1 - P_1 - P_2) - m P_2 - c_1 P_1 P_2$$

As the superior competitor, species 1 has the same equation as it would when living by itself, and thus will reach the same equilibrium since it is totally unaffected by species 2. On the other hand, species 2, can only colonize sites in which both species are absent (the term  $1 - P_1 - P_2$ ) and will be displaced by species 1 (the term  $-c_1 P_1 P_2$ ). What is the invasion criterion for  $P_2$  in terms of  $c_2$  (i.e., how large should  $c_2$  be in order to invade)? [5 pts]

- (3) Show the coexistence equilibrium of the two species and discuss the relationship between the previous invasion criterion for  $P_2$  and the feasibility criterion. [2.5 pts]
- (4) Use stability analysis to show the stability criterion for the coexistence equilibrium. [5 pts]
- (5) In fact, you can show that even with two species, the habitat is still not fully occupied and can thus allow the invasion of a third species with even higher colonization rate. Please expand the model to a three species system (i.e., include  $P_3(t)$ , the least competitive species that will be displaced by both species 1 and 2) following the same logic. [7.5 pts]
- (6) Simulate the model that you wrote above. Run it for 2000 time steps, equal initial occupancy of 0.1, and parameters:  $c_1 = 0.2$ ,  $c_2 = 0.5$ ,  $c_3 = 0.7$ ,  $m = 0.1$ . Report the final equilibrium occupancy of the three species (rounded to three decimal places). [2.5 pts]

### Solution

(1)

$$\frac{dP_1}{dt} = P_1 (c_1 - c_1 P_1 - m)$$

The monoculture equilibrium  $P_1^*$  is 0 or  $1 - \frac{m}{c_1}$

Since  $m$  is always larger than 0 and  $c_1$  cannot be infinite, the species can never fully occupy the habitat (i.e., there will always be unoccupied space left).

(2)

The invasion criterion for  $P_2$  is:

$$\lim_{P_2 \rightarrow 0} \frac{1}{P_2} \frac{dP_2}{dt} \big|_{P_1=P_1^*} = c_2 \left( 1 - \left( 1 - \frac{m}{c_1} \right) - 0 \right) - m - c_1 \left( 1 - \frac{m}{c_1} \right) = \frac{c_2}{c_1} m - c_1 > 0$$

→ For  $P_2$  to invade the monoculture equilibrium of  $P_1$ ,  $C_2 > \frac{c_1^2}{m}$

(3)

$$\frac{dP_1}{dt} = 0 \rightarrow P_1^* = 0, 1 - \frac{m}{c_1}$$

$$\frac{dP_2}{dt} = 0 \rightarrow P_2^* = 0, \frac{m}{c_1} - \frac{c_1}{c_2}$$

If  $P_2$  can invade (i.e.,  $C_2 > \frac{c_1^2}{m}$ ), then  $P_2^*$  is also feasible ( $\frac{m}{c_1} - \frac{c_1}{c_2} > 0$ ) → invasibility guarantees feasibility

(4)

The Jacobian for the internal equilibrium  $E_c$  is:

$$J_{E_c} = \begin{bmatrix} c_1(1 - P_1^*) - m + (-c_1)P_1^* & 0 \\ (-c_2 - c_1)P_2^* & [c_2(1 - P_1^* - P_2^*) - m - c_1P_1^*] + (-c_2)P_2^* \end{bmatrix}$$

- The eigenvalues are:  $-c_1P_1^*$  and  $-c_2P_2^*$
- If  $E_c$  is feasible ( $P_1^*, P_2^* > 0$ ), then it is stable

(5)

The differential equations for the three-species system are:

$$\frac{dP_1}{dt} = c_1 P_1 (1 - P_1) - m P_1$$

$$\frac{dP_2}{dt} = c_2 P_2 (1 - P_1 - P_2) - m P_2 - c_1 P_1 P_2$$

$$\frac{dP_3}{dt} = c_3 P_3 (1 - P_1 - P_2 - P_3) - m P_3 - c_1 P_1 P_3 - c_2 P_2 P_3$$

(6)

The proportion of each species at equilibrium is:

$P_1$	$P_2$	$P_3$
0.500	0.100	0.043

R code

```
library(tidyverse)
```

```
library(deSolve)
```

```
Col_comp_model <- function(times, state, parms){
  with(as.list(c(state, parms)), {
    dP1_dt = c1*P1*(1-P1)-m*P1
    dP2_dt = c2*P2*(1-P1-P2)-m*P2-c1*P1*P2
    dP3_dt = c3*P3*(1-P1-P2-P3)-m*P3-c1*P1*P3-c2*P2*P3

    return(list(c(dP1_dt, dP2_dt, dP3_dt)))
  })
}
```

```

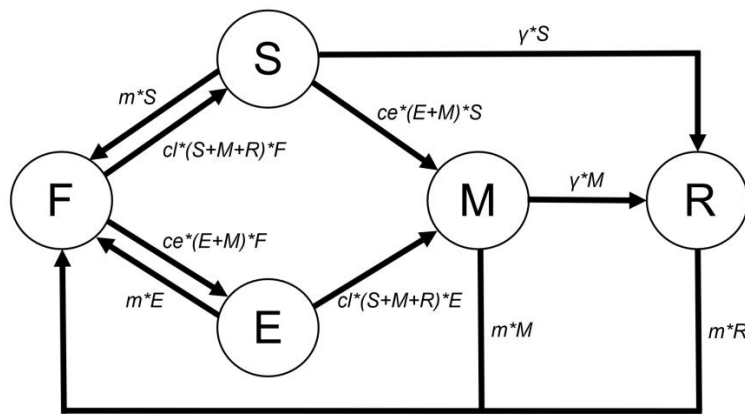
times <- seq(1, 1000, by = 0.1)
parms <- c(c1 = 0.2, c2 = 0.5, c3 = 0.7, m = 0.1)
state <- c(P1 = 0.1, P2 = 0.1, P3 = 0.1)

pop_size <- ode(func = Col_comp_model, times = times, y = state, parms =
parms)
round(tail(pop_size[, -1]), 3)

pop_size %>%
  as.data.frame() %>%
  pivot_longer(cols = -time, names_to = "species", values_to = "N") %>%
  ggplot(aes(x = time, y = N, color = species)) +
  geom_line(size = 1.25) +
  theme_classic(base_size = 14) +
  labs(x = "Time", y = "N") +
  scale_x_continuous(limits = c(0, 1050), expand = c(0, 0)) +
  scale_y_continuous(limits = c(0, max(pop_size[, -1])*1.1), expand = c(0,
0)) +
  scale_color_brewer(name = NULL, palette = "Set1")

```

4. The competition-colonization tradeoff mentioned above is a useful concept in community ecology. However, one critical assumption of the model is that it assumes immediate displacement competition (i.e., species 1 immediately outcompetes species 2 upon its arrival and the two species never co-occur in a local site, not even for a short transient period). To relax this assumption, we need an extra state variable – a mixed-occupancy patch with both species. Fixing this assumption results in an expanded model that can be used to study the dynamics of ecological succession (Pacala & Rees 1998, *Am Nat*), which tracks the transitions between patches belonging to different successional states. See below model diagram.



In this model, there are two types of species: early-successional species (the better colonizer) and late-successional species (the better competitor). The model views succession as the transition among five different states:

- Free state –  $F(t)$ , unoccupied patches.
- Early state –  $E(t)$ , occupied by only the early-successional species.
- Susceptible state –  $S(t)$ , occupied by only the late-successional species but is susceptible to the colonization of the early-successional species because the resource levels have not yet been drawn down below the minimum requirement of the early species.
- Mixed state –  $M(t)$ , occupied by both types of species and in transition to competitive exclusion.

- Resistant state –  $R(t)$ , occupied by only the late-successional species and is resistant to the colonization of the early-successional species because the resource levels have already been drawn down below the minimum requirement of the early species.

Here,  $ce$  is the colonization rate of the early-successional species;  $cl$  is the colonization rate of the late-successional species;  $\gamma$  is the transition rate at which Susceptible and Mixed states turn into the Resistant state, representing the ability of the late-successional species to deplete resources (i.e., a measure of the late species' competitive ability);  $m$  is the disturbance-induced mortality rate, which causes all occupied states to return to the Free state.

- (1) Write out the system of differential equations based on the above flow diagram. [7.5 pts]
- (2) Despite being a five-variable model, we can still gain some insight from analytical analysis. First, define a new state variable  $N_1(t)$ , which represents the proportion of patches with the late-successional species and equals  $S(t) + M(t) + R(t)$ . Write down the equation that captures its dynamics, i.e.,  $dN_1(t)/dt$ . Note that  $S(t) + M(t) + R(t) + E(t) + F(t) = 1$ . [2.5 pts]  
(not part of the exam but you can think about what is the equilibrium occupancy of  $N_1(t)$  and compare this to the original competition-colonization tradeoff model)
- (3) Second, show the monoculture equilibrium of the early-successional species. To do so we only need to consider the model with  $E(t)$  and  $F(t)$ . Note that now  $E(t) + F(t) = 1$ . [2.5 pts]
- (4) Finally, use the equation from question (2) to calculate the invasion criterion for the late-successional species to invade the monoculture equilibrium of the early-successional species. What parameters go into the criterion and how does this result differ from other invasion analysis that you've done before. Why does it makes sense? [5 pts]
- (5) The colonization-competition trade-off suggests that the early-successional species has greater colonization ability than the late-successional species ( $ce > cl$ ), while the latter is better at depleting resources and thus more competitive than the former ( $\gamma > 0$ ). Use the provided parameters ( $ce = 0.8$ ,  $cl = 0.1$ ,  $\gamma = 0.8$ ,  $m = 0.05$ ) and initial conditions ( $S(0) = 0.01$ ,  $E(0) = 0.03$ ,  $M(0) = 0$ ,  $R(0) = 0$ ,  $F(0) = 0.96$ ) to simulate the system dynamics and report the proportions of the five states at equilibrium (rounded to three decimal places). [2.5 pts]
- (6) Reducing the competitive ability ( $\gamma$ ) of the late-successional species may slow down the competitive exclusion of early-successional species. Simulate the system dynamics using the

same parameters and initial conditions in (5) but with  $\gamma = 0.08$ . Compared with the previous results, what difference do you find regarding the Mixed state at equilibrium? Explain why your parameter change produces this result. [2.5 pts]

- (7) Suppose that the community is now under some kind of chronic anthropogenic disturbance and thus the state mortality rate  $m$  has increased by 50% (other parameters and initial conditions remain the same as those in (5)). Which species would benefit most from such disturbance? [2.5 pts]

### Solution

(1)

The system of differential equations are:

$$\frac{dS}{dt} = c_l (S + M + R)F - c_e(E + M)S - \gamma S - mS$$

$$\frac{dE}{dt} = c_e(E + M)F - c_l (S + M + R)E - mE$$

$$\frac{dM}{dt} = c_e(E + M)S + c_l (S + M + R)E - \gamma M - mM$$

$$\frac{dR}{dt} = \gamma M + \gamma S - mR$$

$$\frac{dF}{dt} = m(S + E + M + R) - c_l (S + M + R)F - c_e(E + M)F$$

(2)

The differential equation for the newly-defined state variable  $N_1$  is:

$$\frac{dN_1}{dt} = \frac{dS}{dt} + \frac{dM}{dt} + \frac{dR}{dt} = c_l N_1 (1 - N_1) - mN_1$$



(3)

In the monoculture of the early-successional species, S, M, and R are all 0, and so we get:

$$\frac{dE}{dt} = c_e EF - mE$$

$$\frac{dF}{dt} = mE - c_e EF$$

→ The equilibrium point  $(E^*, F^*) = (1 - \frac{m}{c_e}, \frac{m}{c_e})$

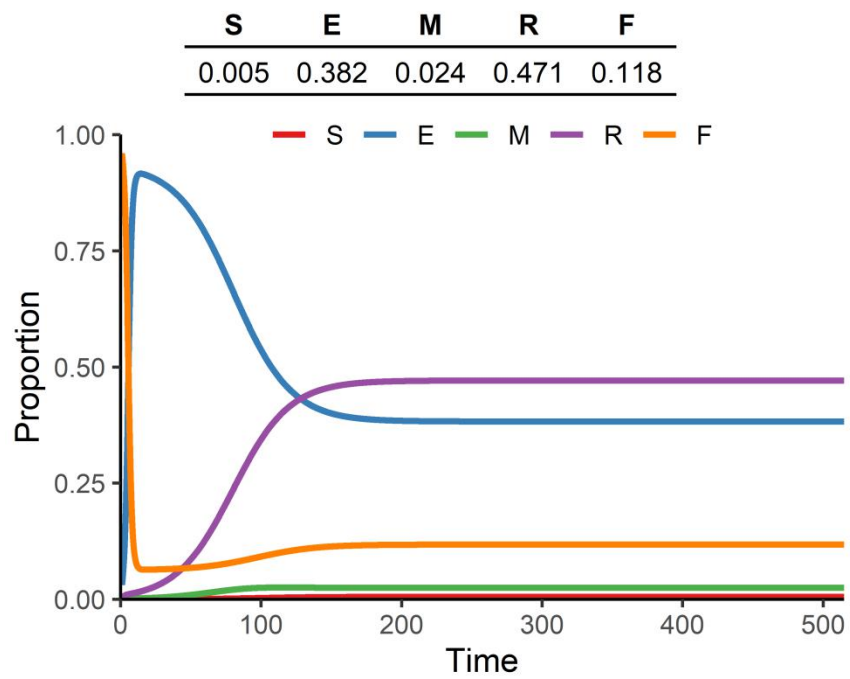
(4)

The invasion criterion for  $N_1$  is:

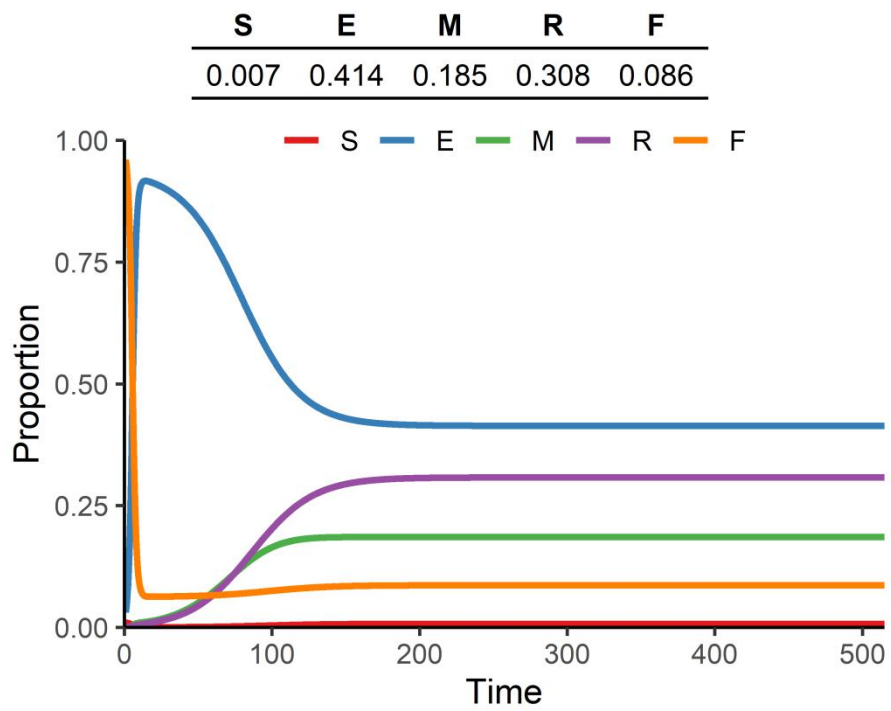
$$\frac{1}{N_1} \frac{dN_1}{dt} = c_l(1 - N_1) - m = c_l - m > 0$$

→  $N_1$  can invade the monoculture of the early-successional species if  $c_l > m$ . Here, the invasion criterion for  $N_1$  is independent of the parameters (traits) related to the early-successional species, which is reasonable because the late-successional species is competitively superior and can always exclude the early-successional species regardless of the traits early-successional species possesses.

(5)

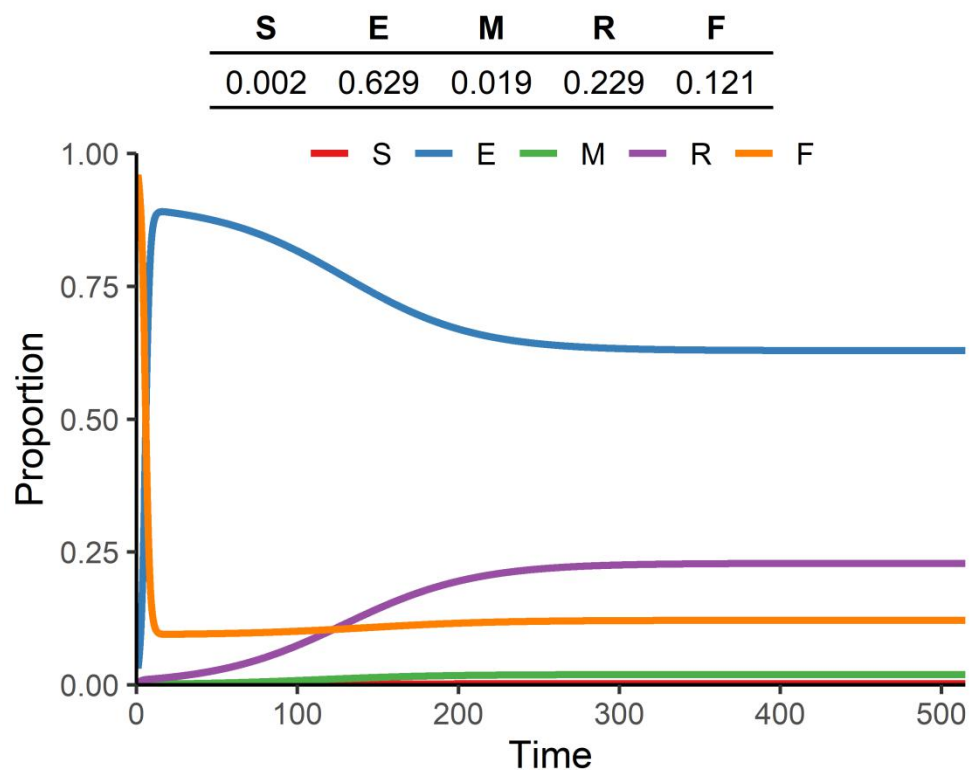


(6)



Compared with the results in (5), the proportion of Mixed state at equilibrium has increased nearly 8-fold from 0.024 to 0.185, suggesting that lowering the competitive ability of late-successional species could promote species coexistence in the same patch.

(7)



Compared with the results in (5), the proportion of Early state at equilibrium has increased from 0.383 to 0.629, whereas that of Resistant state has decreased from 0.471 to 0.229, indicating that disturbance would favor the early-successional species as more unoccupied space is made available for colonization.

## R code

```
library(tidyverse)
library(deSolve)
library(ggpubr)
library(cowplot)

Succession_model_fun <- function(ce, cl, gamma, m) {

  Succession_model <- function(times, state, parms){
    with(as.list(c(state, parms)), {
      dS_dt = cl*(S+M+R)*`F` - ce*(E+M)*S - gamma*S - m*S
      dE_dt = ce*(E+M)*`F` - cl*(S+M+R)*E - m*E
      dM_dt = ce*(E+M)*S + cl*(S+M+R)*E - gamma*M - m*M
      dR_dt = gamma*M + gamma*S - m*R
      dF_dt = m*(S+E+M+R) - cl*(S+M+R)*`F` - ce*(E+M)*`F`

      return(list(c(dS_dt, dE_dt, dM_dt, dR_dt, dF_dt)))
    })
  }

  times <- seq(1, 1000, by = 0.1)
  state <- c(S = 0.01, E = 0.03, M = 0, R = 0, `F` = 0.96)
  parms <- c(ce = ce, cl = cl, gamma = gamma, m = m)

  pop_size <- ode(func = Succession_model, times = times, y = state, parms =
parms)
```

```

P_tab <- ggtexttable(format(as.data.frame(t(round(pop_size[nrow(pop_size),
-1], 3))), nsmall = 3),

                      theme = ttheme("blank", base_size = 12),

                      rows = NULL) %>%

  tab_add_hline(at.row = 1, row.side = "bottom", linewidth = 3, linetype =
1) %>%

  tab_add_hline(at.row = 2, row.side = "bottom", linewidth = 3, linetype =
1)

P_plot <- pop_size %>%
  as.data.frame() %>%
  pivot_longer(cols = -time, names_to = "state", values_to = "N") %>%
  mutate(state = fct_relevel(state, "S", "E", "M", "R", "F")) %>%
  ggplot(aes(x = time, y = N, color = state)) +
  geom_line(size = 1.25) +
  theme_classic(base_size = 14) +
  theme(strip.background = element_blank(),
        strip.placement = "outside",
        legend.title = element_blank(),
        legend.position = c(0.5, 1),
        legend.direction = "horizontal",
        plot.margin = margin(t = 15, r = 5, l = 4)) +
  labs(x = "Time", y = "Proportion") +
  scale_x_continuous(limits = c(0, 515), expand = c(0, 0)) +
  scale_y_continuous(limits = c(0, 1), expand = c(0, 0)) +
  scale_color_brewer(name = NULL, palette = "Set1")

ggarrange(P_tab, P_plot, heights = c(0.15, 0.85), nrow = 2)

```

```
}
```

```
Succession_model_fun(ce = 0.8, cl = 0.1, gamma = 0.8, m = 0.05)
```

```
Succession_model_fun(ce = 0.8, cl = 0.1, gamma = 0.08, m = 0.05)
```

```
Succession_model_fun(ce = 0.8, cl = 0.1, gamma = 0.8, m = 0.05*1.5)
```