

# Equations & R Code

March 22, 2016

Seasonal (within-year) dynamics are modeled as three differential equations:

$$\frac{dN_i}{d\tau} = N_i \epsilon_i f_i(R) \quad (1)$$

$$\frac{dR}{d\tau} = - \sum_{i=1,2} f_i(R) N_i \quad (2)$$

```
## Continuous model
updateDNR <- function(t, DNR, parms){
  with(as.list(c(DNR, parms)), {
    dD1dt = 0
    dD2dt = 0
    dN1dt = N1*eps[1]*(uptake_R(r[1], R, alpha[1], beta[1]))
    dN2dt = N2*eps[2]*(uptake_R(r[2], R, alpha[2], beta[2]))
    dRdt = -1 * (dN1dt/eps[1] + dN2dt/eps[2])
    list(c(dD1dt, dD2dt, dN1dt, dN2dt, dRdt)) #output
  })
}

## Resource uptake function (Hill function)
uptake_R <- function(r, R, alpha, beta){
  return((r*R^alpha) / (beta^alpha + R^alpha))
}
```

where  $i$  denotes species,  $D$  is the dormant (long-lived) biomass state, and  $N$  is the living biomass (fast-growing, shorter-lived) state, and  $\epsilon_i$  is each species' resource-to-biomass conversion efficiency. The growth rate of living biomass is a resource-dependent Hill function,  $f_i(R) = r_i R^{a_i} / (b_i^{a_i} + R^{a_i})$ , where  $r$  is a species' intrinsic growth rate and  $a$  and  $b$  define the curvature of the function. Resource depletion is equal to the sum of each species' consumption,  $\sum_{i=1,2} f_i(R) N_i$ .

At the beginning of each season we start with initial conditions defined as  $V_t$ ,  $W_t$ , and  $Z_t$  for the dormant state, the live state, and the resource, respectively. So for each season, eqs. 1-3 are solved given the initial conditions:

$$D_i(0) = V_{i,t} \quad (3)$$

$$N_i(0) = W_{i,t} \quad (4)$$

$$R(0) = Z_t \quad (5)$$

The consumers transition between  $N$  and  $D$  instantaneously between years. So, at the yearly transition:

$$V_{i,t+1} = \alpha_i N_i(T^-) + D_i(T^-)(1 - \gamma_{i,t})(1 - \eta_i) \quad (6)$$

$$W_{i,t+1} = \beta_i (1 - \alpha_i) N_i(T^-) + \gamma_{i,t} [D_i(T^-) + \alpha_i N_i(T^-)] (1 - \eta_i) \quad (7)$$

$$Z_{t+1} = \theta_i (1 - \alpha_i) N_i(T^-) + \nu R(T^-) + R(T^+) \quad (8)$$

```

## Discrete model
update_DNR <- function(t,DNR,gs,a1,a2,m1,m2,b1,b2,theta1,theta2,c){
  with (as.list(DNR),{
    g1 <- gs[1]
    g2 <- gs[2]
    D1 <- a1*N1 + D1*(1-g1)*(1-m1)
    D2 <- a2*N2 + D2*(1-g2)*(1-m2)
    N1 <- b1*(1-a1)*N1 + g1*(D1+(a1*N1))*(1-m1)
    N2 <- b2*(1-a2)*N2 + g2*(D2+(a2*N2))*(1-m2)
    R <- theta1*(1-a1)*N1 + theta2*(1-a2)*N2 + c*R + Rvector[t]
    return(c(D1, D2, N1, N2, R))
  })
}

```

where  $D(T^-)$ ,  $N(T^-)$ , and  $R(T^-)$  are the densities of each state at the end of the year and  $g$  is a time-fluctuating activation rate that regulates how much dormant biomass is converted to growing-season live biomass each year.  $R(T^+)$  is a randomly generated resource pulse from a log-normal distribution with mean  $R_\mu$  and variance  $R_{\sigma^2}$ . Parameter notations and definitions are in table 1.

Table 1: Definition of model states and parameters. ‘Constant’ parameters do not fluctuate during a simulation, while ‘variable’ parameters do fluctuate through time in a given simulation.

| Parameter      | Definition  |
|----------------|---|
| $N$            | live biomass  |
| $D$            | dormant biomass   |
| $R$            | resource supply   |
| $\alpha$       | allocation fraction of live biomass to seed bank (constant) |
| $\beta$        | live state survivorship (constant)                          |
| $\eta$         | dormant state mortality rate (constant)                     |
| $\epsilon$     | resource-to-biomass efficiency (constant)                   |
| $\gamma$       | dormant-to-live biomass transition fraction (variable)      |
| $\nu$          | resource carry-over fraction (constant)                     |
| $\theta$       | resource recycling fraction (constant)                      |
| $a$            | Hill function power parameter (constant)                    |
| $b$            | Hill function parameter (constant)                          |
| $\rho$         | correlation of species’ responses transition cue (constant) |
| $\sigma_E^2$   | variance of transition cue (constant)                       |
| $R_\mu$        | mean resource pulse, on log scale (constant)                |
| $R_{\sigma^2}$ | variance of annual resource supply, on log scale (variable) |

## Full R Code for Simulations

```
####
#### Initial Conditions, Global Variables, and Parameters -----
####
seasons <- 1000                # number of seasons to simulate
seasons_to_exclude <- 200      # initial seasons to exclude from plots
days_to_track <- 20           # number of days to simulate in odSolve
DNR <- c(D=c(1,1),N=c(1,1),R=10) # initial conditions
Rmu <- 3                       # mean resource pulse (on log scale)
Rsd_annual <- 0                # std dev of resource pulses (on log scale)
sigE <- 2                      # environmental cue variance
rho <- 0                       # environmental cue correlation between species

# Within-season parameters
parms <- list(
  r = c(5,5),                  # max growth rate for each species
  a = c(5,5),                  # rate parameter for Hill function
  b = c(20,20),                # shape parameter for Hill function
  eps = c(0.2,0.2)             # resource-to-biomass efficiency
)

# End-of-season transition parameters
alpha1 <- 0.50                 # live-to-dormant biomass fraction; spp1
alpha2 <- 0.49                 # live-to-dormant biomass fraction; spp2
beta1 <- 0                     # adult survivorship; spp1 (0 if annual, >0 if perennial)
beta2 <- 0                     # adult survivorship; spp2 (0 if annual, >0 if perennial)
eta1 <- 0.1                    # dormant mortality; spp1
eta2 <- 0.1                    # dormant mortality; spp2
```

```

theta1 <- 0                                # resource recycling fraction; spp1
theta2 <- 0                                # resource recycling fraction; spp2
nu <- 0                                    # resource carry-over fraction

####
#### Load relevant libraries -----
####
library('deSolve')
library('mvtnorm')

####
#### Model functions -----
####
## Continuous model
updateDNR <- function(t, DNR, parms){
  with(as.list(c(DNR, parms)), {
    dD1dt = 0
    dD2dt = 0
    dN1dt = N1*eps[1]*(uptake_R(r[1], R, a[1], b[1]))
    dN2dt = N2*eps[2]*(uptake_R(r[2], R, a[2], b[2]))
    dRdt = -1 * (dN1dt/eps[1] + dN2dt/eps[2])
    list(c(dD1dt, dD2dt, dN1dt, dN2dt, dRdt)) #output
  })
}

## Resource uptake function (Hill function)
uptake_R <- function(r, R, a, b){
  return((r*R^a) / (b^a + R^a))
}

## Discrete model
update_DNR <- function(t,DNR,gammas,alpha1,alpha2,eta1,eta2,beta1,beta2,theta1,theta2,nu){
  with (as.list(DNR),{
    g1 <- gammas[1]
    g2 <- gammas[2]
    D1 <- alpha1*N1 + D1*(1-g1)*(1-eta1)
    D2 <- alpha2*N2 + D2*(1-g2)*(1-eta2)
    N1 <- beta1*(1-alpha1)*N1 + g1*(D1+(alpha1*N1))*(1-eta1)
    N2 <- beta2*(1-alpha2)*N2 + g2*(D2+(alpha2*N2))*(1-eta2)
    R <- theta1*(1-alpha1)*N1 + theta2*(1-alpha2)*N2 + nu*R + Rvector[t]
    return(c(D1, D2, N1, N2, R))
  })
}

####
#### Simulate model -----
####
days <- c(1:days_to_track)

# Get "germination" fractions for each year

```

```

getG <- function(sigE, rho, nTime){
  varcov <- matrix(c(sigE, rho*sigE, rho*sigE, sigE), 2, 2)
  e <- rmvnorm(n = nTime, mean = c(0,0), sigma = varcov)
  g <- exp(e) / (1+exp(e))
  return(g)
}

# Loop over seasons
nms <- names(DNR)
gVec <- getG(sigE = sigE, rho = rho, nTime = seasons)
Rvector <- rlnorm(seasons, Rmu, Rsd_annual)
saved_outs <- matrix(ncol=5, nrow=seasons)
for(season_now in 1:seasons){
  output <- ode(y = DNR, times=days,
               func = updateDNR, parms = parms)
  DNR <- output[nrow(output),nms]
  saved_outs[season_now,] <- DNR
  names(DNR) <- nms
  DNR <- update_DNR(season_now, DNR, gVec[season_now,],
                   alpha1=alpha1,alpha2=alpha2,
                   eta1=eta1,eta2=eta2,
                   beta1=beta1,beta2=beta2,
                   theta1=theta1,theta2=theta2,nu=nu)
  names(DNR) <- nms
}
matplot(saved_outs[101:seasons,c(3:4)], type="l",
        xlab="Season", ylab="Abundance",
        main=expression(paste(alpha[1],"= 0.5; ", alpha[2],"=0.49; ", sigma[E],"=0.2")))

```

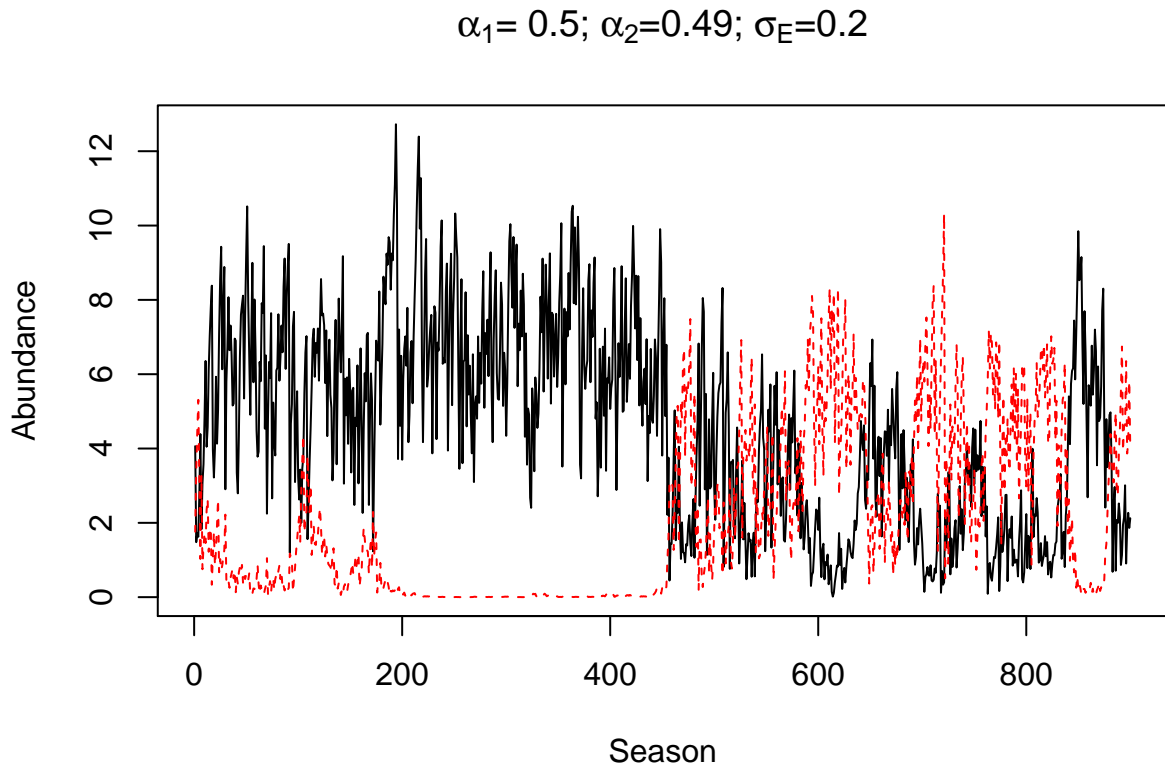


Figure 1: Abundance of both species over 800 seasons. Species have identical resource uptake rates, but differ in their conversion efficiency. This 2 species community represents an annual plant community (no biomass carry-over) with no resource recycling.