

# Tilman's Resource Competition : 2 species 2 resources

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This script allows to visualize the dynamics of two species depending competing for two resources (Tilman 1982). You might want to have a look on the [course notes](#) before going any further.

```
library("deSolve")
library("FME")
```

## Function and parameter definitions

Parameters for growth are now given for both species  $N_1$  and  $N_2$ . In order to be callable for both species, the function `Growth` now receives species-specific parameter as an input argument ( in [the 1 species case](#), those parameters where “global”, here they are “local”).

```
pars<-c(
  # Populations
  mN1 = .1      , # mortality N1
  mN2 = .15     , # mortality N2
  # param for growth
  # N1
  mu1 = .5      , # Max Growth

  limN1R1 = 40  , # Half-Saturation R1 for N1
  limN1R2 = 40  , # Half-Saturation R2 for N1
  gtype1 = 1    , # "essential"
  a11     = .6  , # Resource preference for R1, N1 [0-1]

  # N2
  mu2 = .5      , # Max Growth
  limN2R1 = 50  , # Half-Saturation R1 for N2
  limN2R2 = 50  , # Half-Saturation R2 for N2
  gtype2 = 3    , # "substitutive"
  a21     = .4  , # Resource preference for R1, N2 [0-1]

  # Resources
```

```

g1 = 60      , # Supply R1 (max R1 if no consumption)
g2 = 40      , # Supply R2 (max R2 if no consumption)
gT = 10      , # Relaxation time towards max Conc
gnoisefactor = 5, # Signal to noise ratio

# Initial conditions
N1_0 = 10    , # Initial population N1
N2_0 = 30    , # Initial population N2
R1_0 = 50    , # Initial stock R1
R2_0 = 50    , # Initial stock R2
# Simulation
dt=.1,
TOL=0.05
)

Growth<- function (R1,R2,Pp,hneed=F, gtype=1){#'essential') {
  # Pp gives the species parameters
  # * limR1
  # * limR2
  # * mu
  # The 'with' function executes the code in {} with elements of the list (first argument)
  # included as part of the local environment
  with (as.list(Pp), {
    fR1 <- R1 / (R1 + limR1)
    fR2 <- R2 / (R2 + limR2)
    if (gtype==1){#'essential'){
      #####
      # Essential #
      #####
      f <- mu * pmin(fR1,fR2)
      h1 <- a
      h2 <- (1-a)
      casestring<<-("Essential")
    } else if (gtype==2){#'interactiveEssential'){
      #####
      # Interactive Essential #
      #####
      f <- mu * fR1*fR2
      a<-.2
      h1 <- (a)
      h2 <- (1-a)
      casestring<<-("InteractiveEssential")
    } else if (gtype==3){#'substitutive'){
      #####
      # Perfectly Substitutive #
      #####
      f <- mu * (R1+R2)/ ( R1+R2 + limR1+ limR2 )
      h1 <- R1/(R1+R2)
      h2 <- R2/(R1+R2)
      casestring<<-("perfectlySubstitutive")
    } else if (gtype==4){#'complementary'){

```

```
#####
# Complementary #
#####
f <- mu * ((R1+R2+R1*R2/10)/ (R1+R2+R1*R2/10+limR1+limR2))
h1 <- R1/(R1+R2)
h2 <- R2/(R1+R2)
} else if (gtype==5){#'antagonistic'}{
#####
# Antagonistic #
#####
f <- mu * ((R1+R2-R1*R2/80)/ (R1+R2-R1*R2/80+limR1+limR2))
h1 <- R1/(R1+R2)
h2 <- R2/(R1+R2)
casestring<-("Antagonistic")
} else if (gtype==6){#'switching'}{
#####
# Switching #
#####
f <- mu * pmax(R1,R2)/ (pmax(R1,R2)+ limR1+limR2 )

h1 <- R1/(R1+R2)
h2 <- R2/(R1+R2)
  if (R1>R2){
    h1 <- 1
  } else {
    h1 <- 0
  }
  h2<-1-h1
}
  if (hneed){
    return(c(f=f,h1=h1,h2=h2))
  } else {
    return(f)
  }
})
}
```

```
simpleg <- function (t, X, parms) {
  with (as.list(parms), {
    N1 <- X[1]
    N2 <- X[2]
    R1 <- X[3]
    R2 <- X[4]

    # Return the growth rate and consumption vectors for N1
    pN1<-c( limR1 = limN1R1 ,
            limR2 = limN1R2 ,
            mu    = mu1      ,
            a     = a11      )

    G1<-Growth(R1,R2,pN1,T,gtype=gtype1)
    f1<-G1["f"]
    h11<-G1["h1"]
    h12<-G1["h2"]
  })
}
```

```

# Return the growth rate and consumption vectors for N2
pN2<-c( limR1 = limN2R1 ,
        limR2 = limN2R2 ,
        mu    = mu2      ,
        a      = a21      )

G<-Growth(R1,R2,pN2,T,gtype=gtype2)
f2<-G["f"]
h21<-G["h1"]
h22<-G["h2"]

# Time derivatives
dN1 <- N1 * (f1 - mN1)
dN2 <- N2 * (f2 - mN2)

supply1 = (g1-R1)/gT ## runif(1,0,g1/gnoisefactor)
supply2 = (g2-R2)/gT ## runif(1,0,g1/gnoisefactor)

dR1 <- supply1 - N1*f1*h11 - N2*f2*h21
dR2 <- supply2 - N1*f1*h12 - N2*f2*h22

# Return the time derivative
return(list(c(dN1, dN2, dR1 , dR2)))
})
}

```

## A first simulation

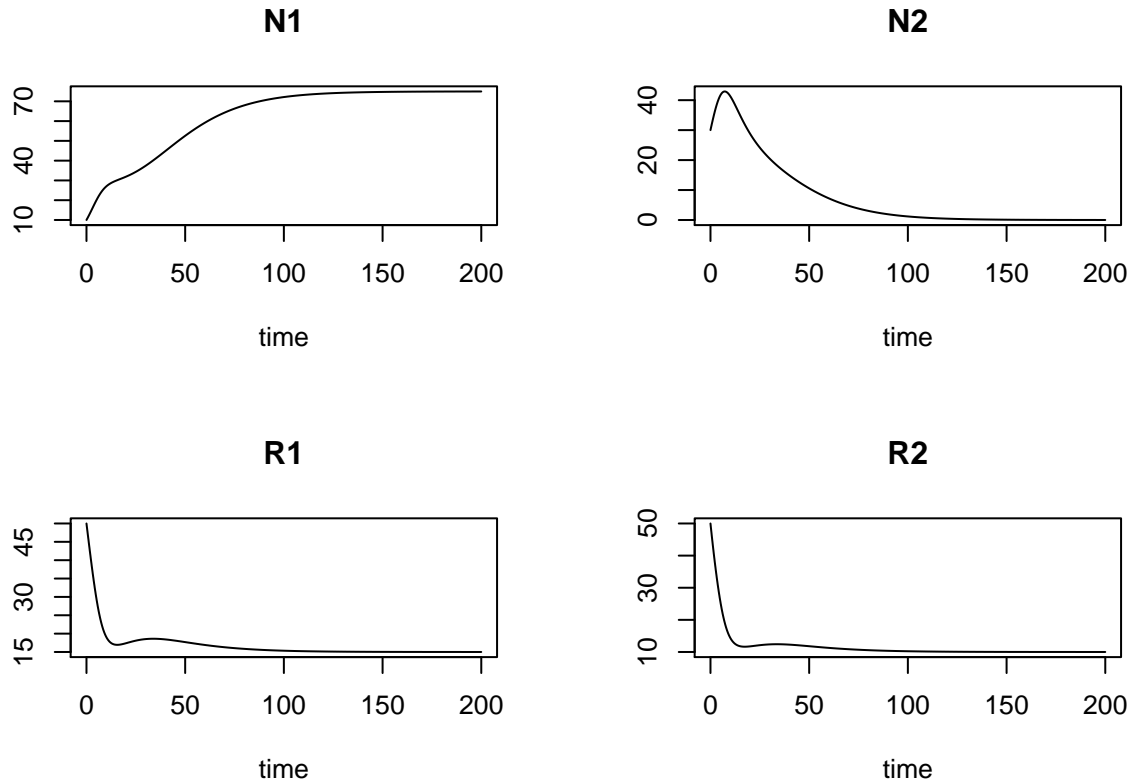
As before we start with a dynamic run

```

X0 <- with(as.list(pars),c(N1_0,N2_0,R1_0,R2_0))
times <- seq(0, 200, by = pars["dt"]) # output wanted at these time intervals

out <- ode(y = X0, times = times, func = simpleg, parms = pars,method = "euler")
colnames(out)<-c("time","N1","N2","R1","R2")
plot(out)

```



## Exploration of the resource space

We'll use the steady simulation to illustrate competition, trajectories and equilibrium on the resource plane. First let us compute the growth values over the resource plane for  $N_1$  and  $N_2$ .

```
#outsteady<-steady(y = X0, time=c(0,Inf),func = simpleg, parms = pars, method= "runsteady")
#outs <- outsteady$y
#names(outs)<-c("N1", "N2", "R1", "R2")

R1space <- seq(0,80, length=80)
R2space <- seq(0,80, length=80)

with (as.list(pars), {
  pN1 <-c( limR1 = limN1R1 ,
           limR2 = limN1R2 ,
           mu    = mu1,
           a =a11 )
  pN2 <-c( limR1 = limN2R1 ,
           limR2 = limN2R2 ,
           mu    = mu2,
           a =a11 )
})

f1space <- outer(R1space,R2space,Growth,Pp=pN1,gtype=pars["gtype1"])
f2space <- outer(R1space,R2space,Growth,Pp=pN2,gtype=pars["gtype2"])
```

## PLOT 1 : Trajectories

```

# ZNGI for N1
contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),col="red",lty = "dotted", labels="ZNGI :
      lwd = 3,
      vfont = c("sans serif", "plain"),
      labcex=1.5,
      xlab = "R1",
      ylab="R2")

# ZNGI for N2
contour(R1space ,R2space ,f2space,levels=as.vector(pars["mN2"]),col="red",lty = "dotted", labels="ZNGI :

# trajectories of the dynamic simulation
lines(out[, "R1"],out[, "R2"] )
points(out[1,"R1"],out[1,"R2"],pch = 19)

# Equilibrium points and resource supply point
points(out[nrow(out), "R1"],out[nrow(out), "R2"],col='red',pch = 19)
#points(outs["R1"],outs["R2"],col='red',cex=2.5)
points(pars["g1"],pars["g2"],col='blue',cex=1.5,bg='blue',pch=21)

# as before, function that display a trajectory for a given set of initial condition
fCRL<-function(parinit){
  X0 <- with(as.list(parinit),c(N1_0,N2_0,R1_0,R2_0))
  out<- ode(y = X0, times = times, func = simpleg, parms = pars,method="euler")
  colnames(out)<-c("time", "N1", "N2", "R1", "R2")

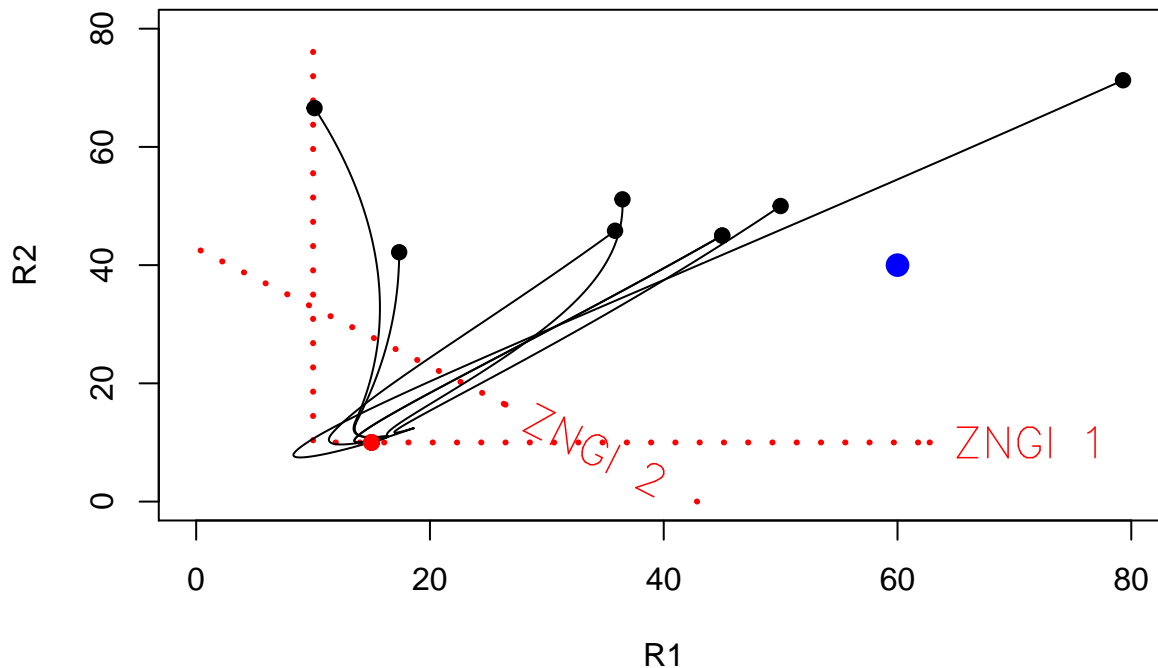
  lines(out[, "R1"],out[, "R2"] )
  points(out[1,"R1"],out[1,"R2"],pch = 19)
  points(out[nrow(out), "R1"],out[nrow(out), "R2"],col='red',pch = 19)
  return(c("R1eq"=out[nrow(out), "R1"], "R2eq"=out[nrow(out), "R2"]))
}

# how initial condition should be perturbed
parRange <- matrix(nr = 4, nc = 2, c(0.2, 0.2, 10,10 ,
                                     50, 50, 80,80 ),
                  dimnames = list(c("N1_0","N2_0","R1_0","R2_0"), c("min", "max")))
print(parRange)

##      min max
## N1_0  0.2  50
## N2_0  0.2  50
## R1_0 10.0  80
## R2_0 10.0  80

# the main call to perturbate parameter and display multiple trajectories
CRL<-modCRL(fCRL,parRange=parRange,num = 5)

```



## PLOT2 : perturbation on the supply point

Instead of perturbing initial conditions, we now perturbate supply point value. You'll see that the position of the supply point determines the position of the equilibrium point somewhere over a *ZNGI*

```
fCRL<-function(parinit){
  parsl<-pars
  parsl[names(parinit)]<-parinit

  X0 <- with(as.list(parsl),c(N1_0,N2_0,R1_0,R2_0))

  out<- ode(y = X0, times = times, func = simpleg, parms = parsl,method="euler")
  colnames(out)<-c("time","N1","N2","R1","R2")

  points(parsl["g1"],parsl["g2"],col='blue',cex=1.5,bg='blue',pch=21)

  lines(c(parsl["g1"],out[length(times),"R1"]),c(parsl["g2"],out[length(times),"R2"]), lty=2 )
  points(out[1,"R1"],out[1,"R2"],pch = 19)
  points(out[nrow(out),"R1"],out[nrow(out),"R2"],col='red',pch = 19)
  return(c("R1eq"=out[nrow(out),"R1"], "R2eq"=out[nrow(out),"R2"]))
}

parRange <- matrix(nr = 2, nc = 2, c(0, 0, 80,80 ,
                                     50, 50, 80,80 ),
                  dimnames = list(c("g1","g2"), c("min", "max")))

parRange
```

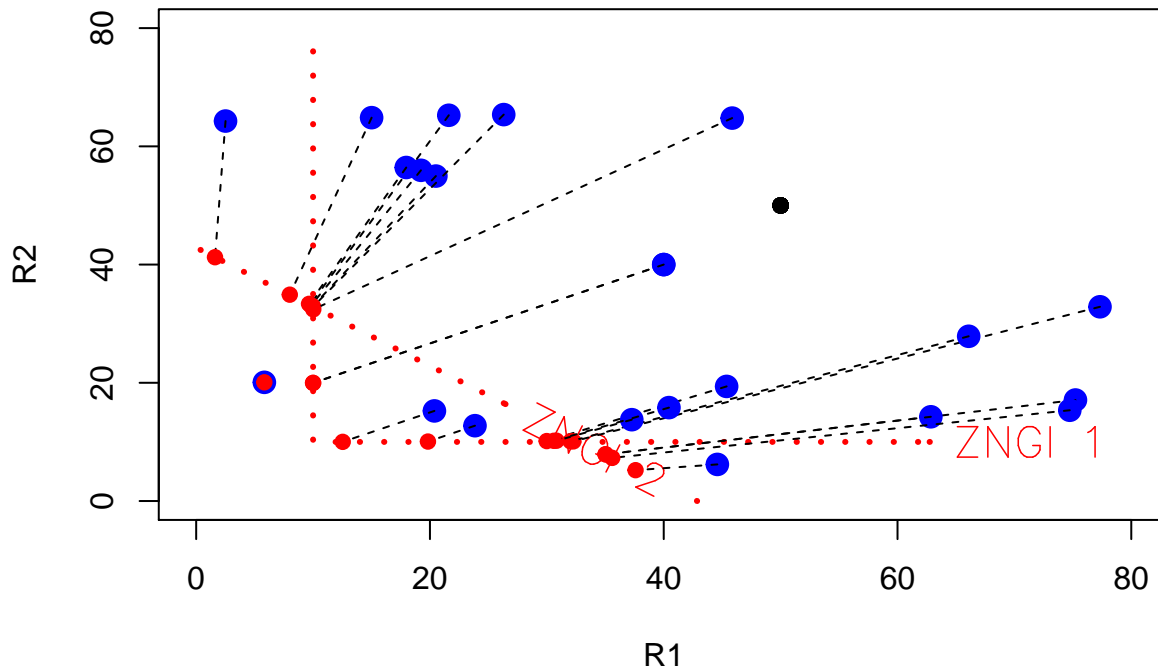
```
##      min max
## g1   0  80
## g2   0  80
```

```

contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),col="red",lty = "dotted", labels="ZNGI 1",
        lwd = 3,
        vfont = c("sans serif", "plain"),
        labcex=1.5,
        xlab = "R1",
        ylab="R2")
contour(R1space ,R2space ,f2space,levels=as.vector(pars["mN2"]),col="red",lty = "dotted", labels="ZNGI 2",
        lwd = 3,
        vfont = c("sans serif", "plain"),
        labcex=1.5,
        xlab = "R1",
        ylab="R2")

CRL<-modCRL(fCRL,parRange=parRange,num = 20)

```



##

PLOT3: perturbation on the supply point - Cohabitation ?

Finally, we will plot the supply point with a certain color, according to the results of competition at equilibrium:  
Which species survives? Is cohabitation possible ?

```

if (TRUE) {

fCRL<-function(parinit){
  pars1<-pars
  pars1[names(parinit)]<-parinit

  X0 <- with(as.list(pars1),c(N1_0,N2_0,R1_0,R2_0))

  out<- ode(y = X0, times = times, func = simpleg, parms = pars1,method="euler")
  colnames(out)<-c("time","N1","N2","R1","R2")

  # Give a color to the points according to surviving species
  N1final <- out[length(times),"N1"]
  N2final <- out[length(times),"N2"]

  TOL=pars["TOL"]

  if (N1final> TOL & N2final> TOL) {

```



```

COL="blue" # Cohabitation
}
if (N1final > TOL & N2final <= TOL) {
  COL="red" # only N1 survives
}
if (N1final <= TOL & N2final > TOL) {
  COL="green" # only N2 survives
}
if (N1final <= TOL & N2final <= TOL) {
  COL="Black" # No survival
}

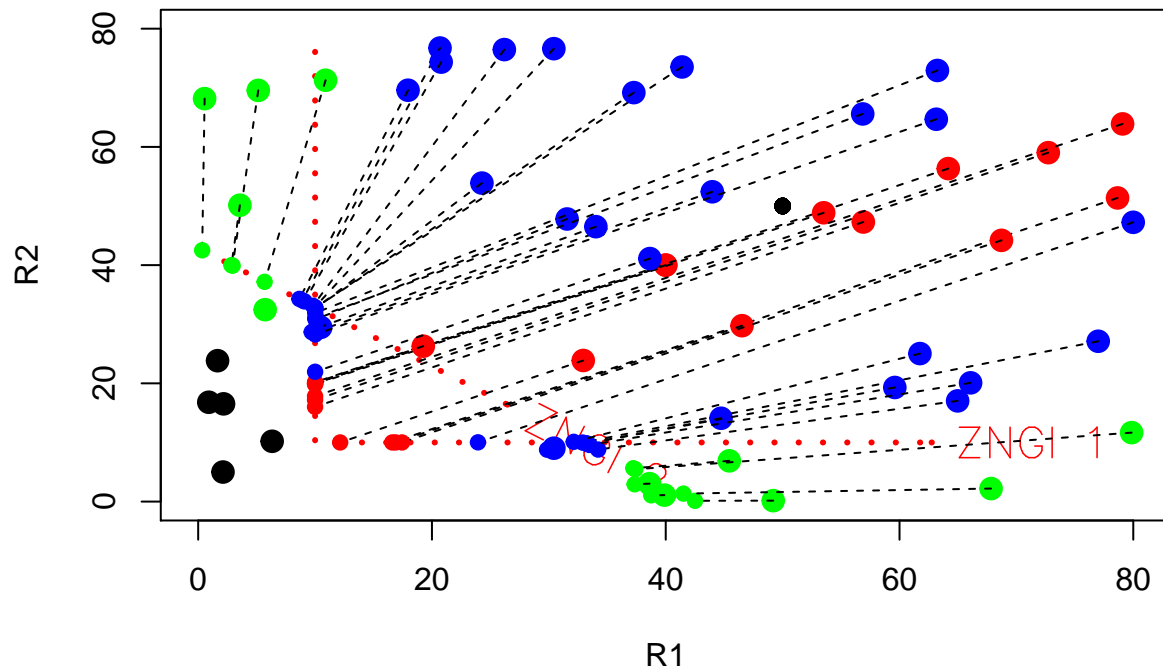
points(parsl["g1"],parsl["g2"],col=COL,cex=1.5,bg=COL,pch=21)
lines(c(parsl["g1"],out[length(times),"R1"]),c(parsl["g2"],out[length(times),"R2"]) , lty=2 )
points(out[1,"R1"],out[1,"R2"],pch = 19)
points(out[nrow(out),"R1"],out[nrow(out),"R2"],col=COL,pch = 19)
return(c("R1eq"=out[nrow(out),"R1"], "R2eq"=out[nrow(out),"R2"]))
}

parRange <- matrix(nr = 2, nc = 2, c(0, 0, 80,80 ,
                                     50, 50, 80,80 ),
                  dimnames = list(c("g1","g2"), c("min", "max")))
parRange

contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),col="red",lty = "dotted", labels="ZNG")
  lwd = 3,
  vfont = c("sans serif", "plain"),
  labcex=1.5,
  xlab = "R1",
  ylab="R2")
contour(R1space ,R2space ,f2space,levels=as.vector(pars["mN2"]),col="red",lty = "dotted", labels="ZNG")

CRL<-modCRL(fCRL,parRange=parRange,num = 50)
}

```



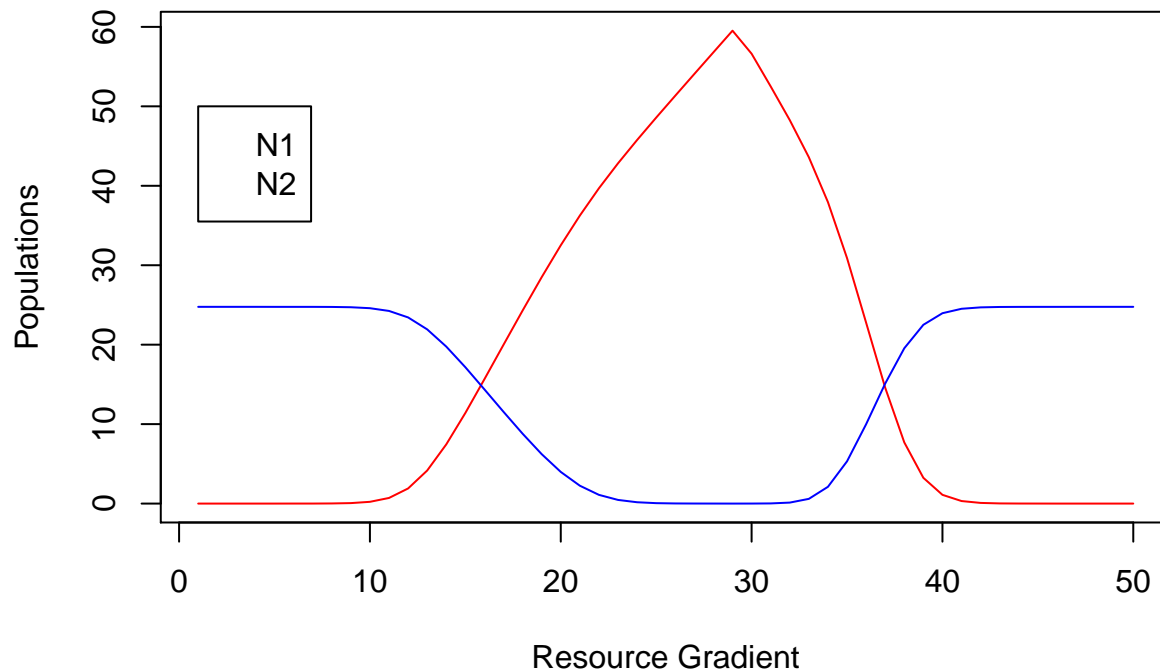
## Exercice

```
fCRL<-function(parinit){
  parsl <- pars
  parsl[names(parinit)]<-parinit
  out <- ode(y = X0, times = times, func = simpleg, parms = parsl,method="euler")
  colnames(out) <- c("time","N1","N2","R1","R2")
  return(out[nrow(out),])}

g1grad <- seq (0,80,length=50)
g2grad <- seq (80,0,length=50)
parInput <- cbind(g1grad,g2grad)
colnames(parInput)<-c("g1","g2")

CRL <- modCRL(fCRL,parInput=parInput,sensvar=c('N1','N2'))

plot (x=1:50, y=CRL$N1 , type = 'l' , col= "red", ylab="Populations", xlab="Resource Gradient")
lines (x=1:50, y=CRL$N2 , col= "blue")
legend(1,50 , c('N1','N2'), col=c("red","blue"))
```

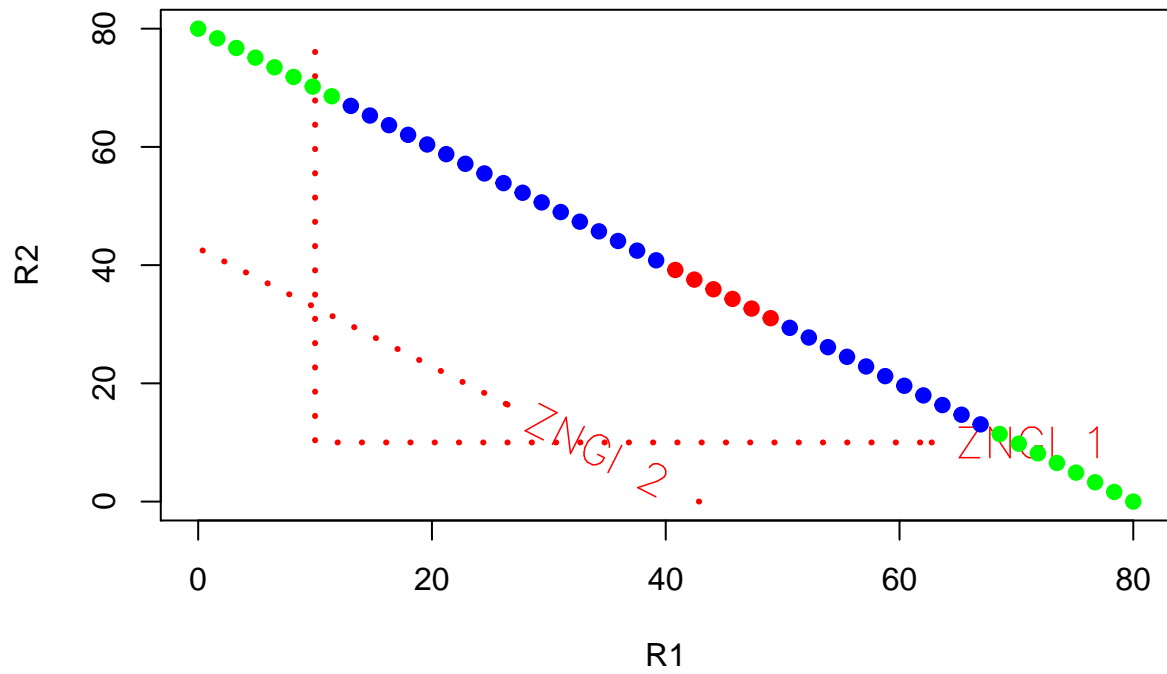


```
communityCases<-apply(CRL,1,function(x){
  N1<-x["N1"]
  N2<-x["N2"]
  TOL<-.05
  if (N1> TOL & N2> TOL) {
    COL="blue" # Cohabitation
  }
  if (N1 > TOL & N2 <= TOL) {
    COL="red" # only N1 survives
  }
  if (N1 <= TOL & N2> TOL) {
    COL="green" # only N2 survives
  }
  if (N1 <= TOL & N2 <= TOL) {
    COL="Black" # No survival
  }
  return(COL)
})

contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),col="red",lty = "dotted", labels="ZNGI",
  lwd = 3,
  vfont = c("sans serif", "plain"),
  labcex=1.5,
  xlab = "R1",
  ylab="R2")

contour(R1space ,R2space ,f2space,levels=as.vector(pars["mN2"]),col="red",lty = "dotted", labels="ZNGI",
  lwd = 3,
  vfont = c("sans serif", "plain"),
  labcex=1.5,
  xlab = "R1",
  ylab="R2")

points(x = CRL$g1, y = CRL$g2, col= communityCases,pch=19)
```



## References

Tilman, David. 1982. *Resource Competition and Community Structure*. Princeton university press.