

Tilman's Resource Competition : 1 species 2 resources

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

```
library("deSolve") # For solving differential equations
library("FME")     # Toolbox to play with model perturbation, sensitivity analysis, etc..
```

Framework

Our system is defined at any given time by 3 state variables :

- N_1 (the population),
- R_1 and R_2 (the ressources).

The growth of N_1 will depend on the availability of both resources in a specific way, as defined in the function `growth1`.

Parameters

All parameters that will be used later are given in a vector (those used in the growth function, but also those used for initial conditions, resource supply, etc ..)

```

pars<-c(
  # 1 Population
  mN1 = .1 , # mortality N1
  ## Params for growth
  mu1 = .5 , # Max Growth
  kN1R1 = 30 , # Half-Saturation R1
  kN1R2 = 40 , # Half-Saturation R2
  # Resources supply
  g1 = 80 , # Supply R1 (max R1)
  g2 = 40 , # Supply R2 (max R2)
  gT = 10 , # Relaxation time towards max Conc
  # Initial conditions
  N1_0 = 10 , # Initial population N1
  R1_0 = 50 , # Initial stock R1
  R2_0 = 50 , # Initial stock R2
  # Simulation
  duration = 100,
  dt=.1
)

```

The growth function

The main growth function `growth1` can take different form, representing different kind of resource (cf. lectures). Currently, we'll just switch to one or another form by commenting/uncommenting part of the code.

`growth1` requires three arguments :

- R1 and R2 are the two resources availabilities
- `hneed` is a flag. If `hneed=FALSE`, the function returns only the growth rate. If `hneed=TRUE`, the function also returns `h1` and `h2`, the components of the resource consumption vector.

```

growth1<- function (R1,R2,hneed=F) {
  with (as.list(pars), {
    f1R1 <- R1 / (R1 + kN1R1)
    f1R2 <- R2 / (R2 + kN1R2)

    #####
    # Essential #
    # Liebig's law of the minimum. If one ressource is lacking
    #####

    # f1 <- mu1 * pmin(f1R1,f1R2)
    # a<-.5
    # h1 <- a
    # h2 <- (1-a)
    #
    # casestring<-("Essential")

    #####
    # Interactive Essential #
    #####

    # f1 <- mu1 * f1R1*f1R2
  })
}

```

```

# a<-.2
# h1 <- (a)
# h2 <- (1-a)

casestring<<-("InteractiveEssential")

#####
# Perfectly Substitutive
#####

# f1 <- mu1 * (R1+R2)/ ( R1+R2 + kN1R1+ kN1R2 )
# h1 <- R1/(R1+R2)
# h2 <- R2/(R1+R2)
# casestring<<-("PerfectlySubstitutive")

#####
# Complementary #
#####

# f1 <- mu1 * ((R1+R2+R1*R2/10)/ (R1+R2+R1*R2/10+kN1R1+kN1R2))
# h1 <- R1/(R1+R2)
# h2 <- R2/(R1+R2)

#####
# Antagonistic
#####
f1 <- mu1 * ((R1+R2-R1*R2/80)/ (R1+R2-R1*R2/80+kN1R1+kN1R2))
h1 <- R1/(R1+R2)
h2 <- R2/(R1+R2)
casestring<<-("Antagonistic")

#####
# Switching
#####

# f1 <- mu1 * pmax(R1,R2)/ (pmax(R1,R2)+ kN1R1+kN1R2 )
#
# h1 <- R1/(R1+R2)
# h2 <- R2/(R1+R2)
# if (R1>R2){
#   h1 <- 1
# } else {
#   h1 <- 0
# }
# h2<-1-h1

if (hneed){
  return(c(f1=f1,h1=h1,h2=h2))
} else {
  return(f1)
}
})

```

```
}
```

Time Derivatives

The following function `simpleg` provides the time derivatives for the state variables, gathered in one vector `X`, in order to compute how the system evolves in time. Those time derivatives depend on the current state, and are controlled by the parameters and the form of the growth function.

```
simpleg <- function (t, X, parms) {  
  with(as.list(parms), {  
    N1 <- X[1]  
    R1 <- X[2]  
    R2 <- X[3]  
  
    # Get the growth rate.  
    # Because the third argument is "True", G is a vector with three named components.  
    # (see definition of growth1)  
    G<-growth1(R1,R2,T)  
    f1<-G["f1"]  
    h1<-G["h1"]  
    h2<-G["h2"]  
  
    dN1 <- N1 * (f1 - mN1) # growth minus mortality  
    dR1 <- (g1-R1)/gT - N1 * (f1 )* h1 # supply minus consumption  
    dR2 <- (g2-R2)/gT - N1 * (f1 )* h2 # supply minus consumption  
  
    # Return the time derivative, the list structure is required by the solving package  
    return(list(c(dN1, dR1 , dR2)))  
  })  
}
```

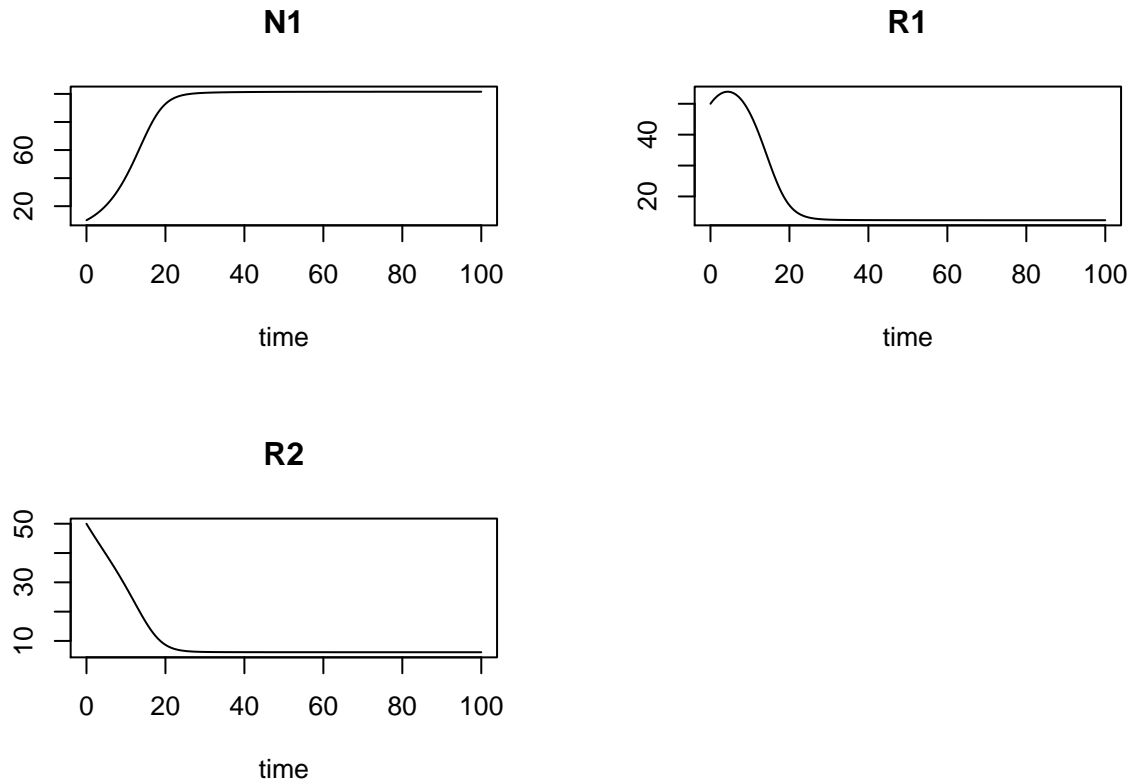
Dynamic simulation

In the following, we

- define the initial conditions `X0`,
- define a number of time step, set a temporal framework
- run first a dynamic simulation, solving the problem in time, ie. looking at the evolution of the population and resources.

```
X0 <- with(as.list(pars),c(N1_0,R1_0,R2_0))  
  
# time intervals at which we want the outputs  
times <- with(as.list(pars),seq(0, duration, by = dt))  
  
# function ode is the solver, it computes the dynamic simulation.  
library(deSolve)  
out <- ode(y = X0, times = times, func = simpleg, parms = pars,method = "euler")  
  
# this give names to the simulation output
```

```
colnames(out)<-c("time", "N1", "R1", "R2")
plot(out)
```



Steady-state solution

Next, we compute directly the steady-state solution, ie the value of state variables for which the time derivative are nul: *growth* compensate for *mortality*, and resource *supply* compensate for *consumption*. The system is balanced, at equilibrium.

The values correspond to the last values of the dynamic run, but they were computed faster, from theoretical considerations, rather than waiting for the system to reach equilibrium by itself.

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

```
##           N1           R1           R2
## 101.554944  12.296704   6.148352
```

Growth on the resource plane

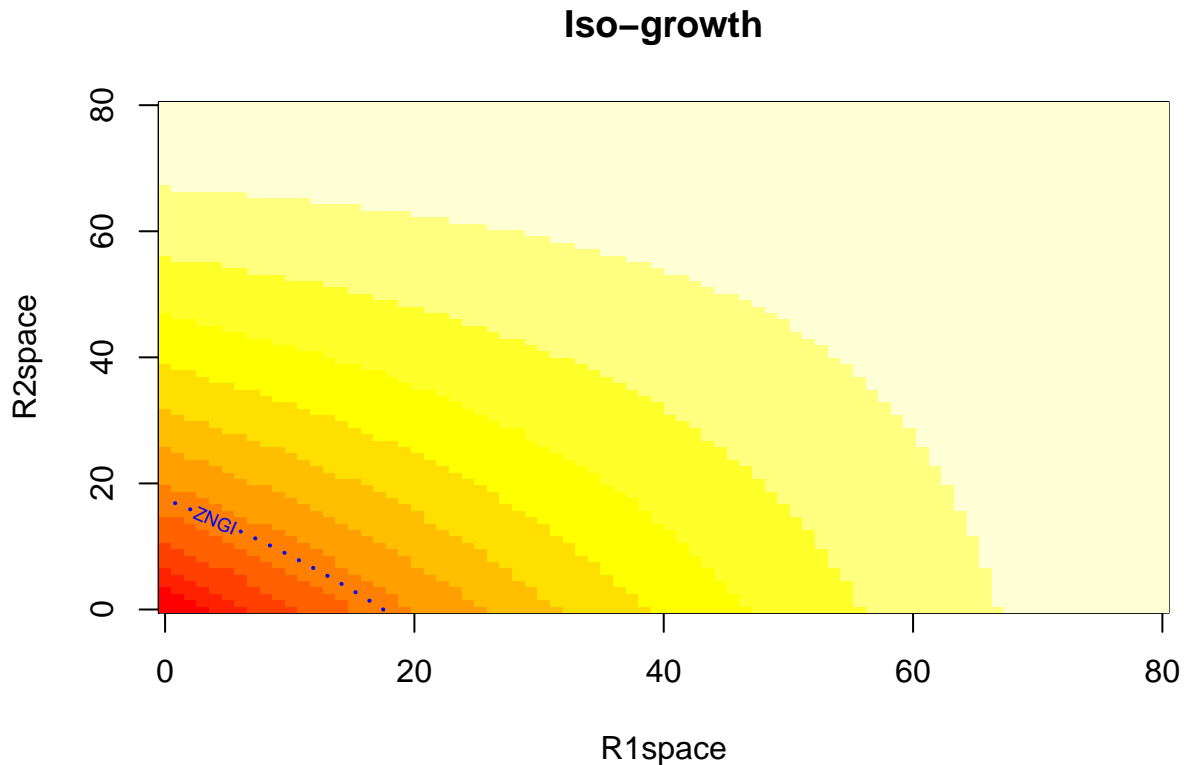
Here, we want to explore how the equilibrium point (such as obtained above) depends on the growth function parameters and initial conditions. The locus of different equilibrium points, in the resource plane (with axis R_1 and R_2), is called the *zero net growth isoline*, or *ZNGI*.

First, we compute growth rates for all values of R_1 and R_2 and display it with colour. Second we highlight the location where growth rate equals mortality rate.

```
# Defining the extent of the ressource space to explore
R1space <- seq(0,80, length=80)
R2space <- seq(0,80, length=80)

# this function evaluate growth 1 for every value of (R1space,R2space)
f1space <- outer(R1space,R2space,growth1)
# First we plot the contour
image(R1space ,R2space ,f1space,main="Iso-growth")

# then we add the line were growth is equal to mortality (= the value in pars["mN1"])
contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),add=T,col="blue",lty = "dotted", labels=
```



Trajectories

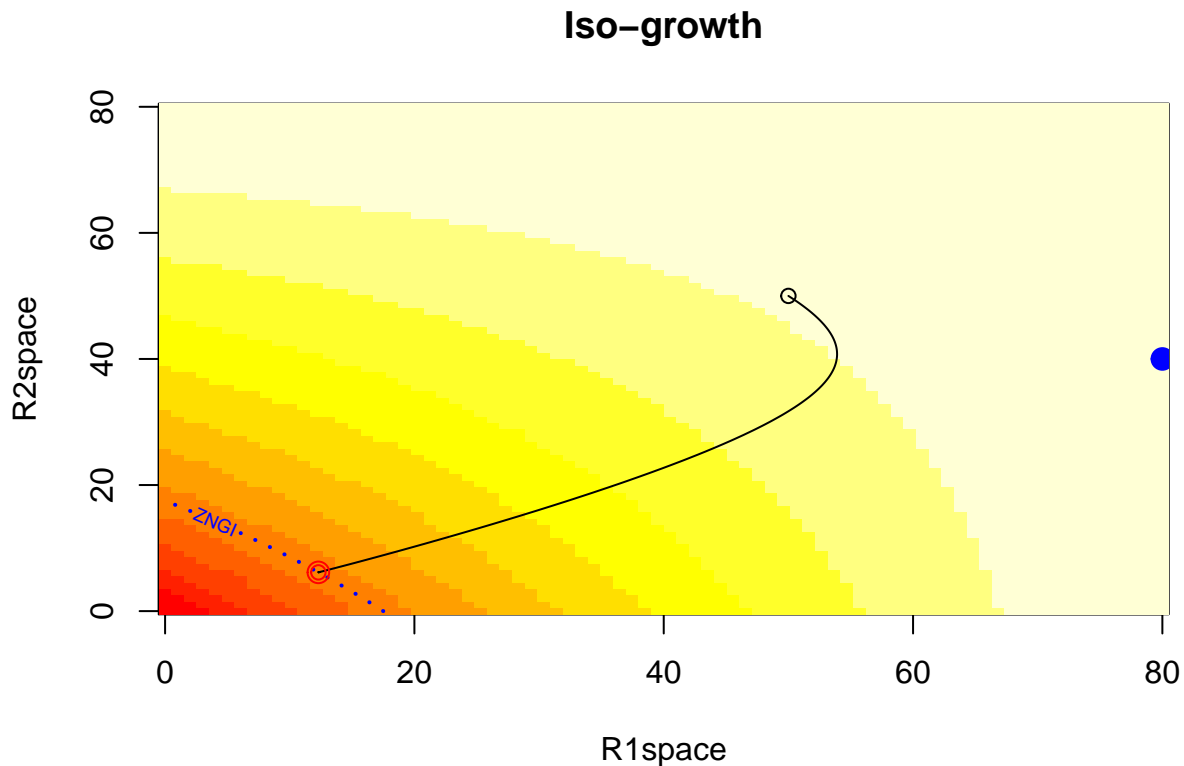
Here we will visualize the trajectory of the simulation we computed just above.

```
image(R1space ,R2space ,f1space,main="Iso-growth")
contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),
        add=T,col="blue",lty = "dotted", labels="ZNGI",lwd=2)

# Now, we plot R1 and R2 from the dynamic solution
lines(out[, "R1"],out[, "R2"])
# highlight the first values of R1 and R2
points(out[1,"R1"],out[1,"R2"])
# the last values
points(out[nrow(out), "R1"],out[nrow(out), "R2"],col='red')
```

```
points(outs["R1"],outs["R2"],col='red',cex=1.5)

# Locate the Supply Point
points(pars["g1"],pars["g2"],col='blue',cex=1.5,bg='blue',pch=21)
```



Perturbations

Finally, to illustrate that this point is a stable equilibrium point we will use the `modCRL` function from the FME package (Soetaert and Petzoldt 2010), to perturbate initial conditions and display corresponding trajectories. The `modCRL` function (type `?ModCRL`) needs a transfer function (`fCRL` below) that will return something according to the parameters received in argument. The function `modCRL` generates perturbation of the parameters (within some range given in `parRange`), calls the transfer function for each parameter set and stores the result. In the present case, it is the transfer function `fCRL` that directly displays the trajectory on the plot.

```
# Just reproduce the same plot as above
image(R1space ,R2space ,f1space,main="Iso-growth")
contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),
        add=T,col="blue",lty = "dotted", labels="ZNGI",lwd=2)
points(pars["g1"],pars["g2"],col='blue',cex=1.5,bg='blue',pch=21)

# define the function to be used by modCRL
fCRL<-function(parinit){
  X0 <- with(as.list(parinit),c(N1_0,R1_0,R2_0))
  out<- ode(y = X0, times = times, func = simpleg, parms = pars,method="euler")
  colnames(out)<-c("time","N1","R1","R2")

  lines(out[, "R1"],out[, "R2"] )
```

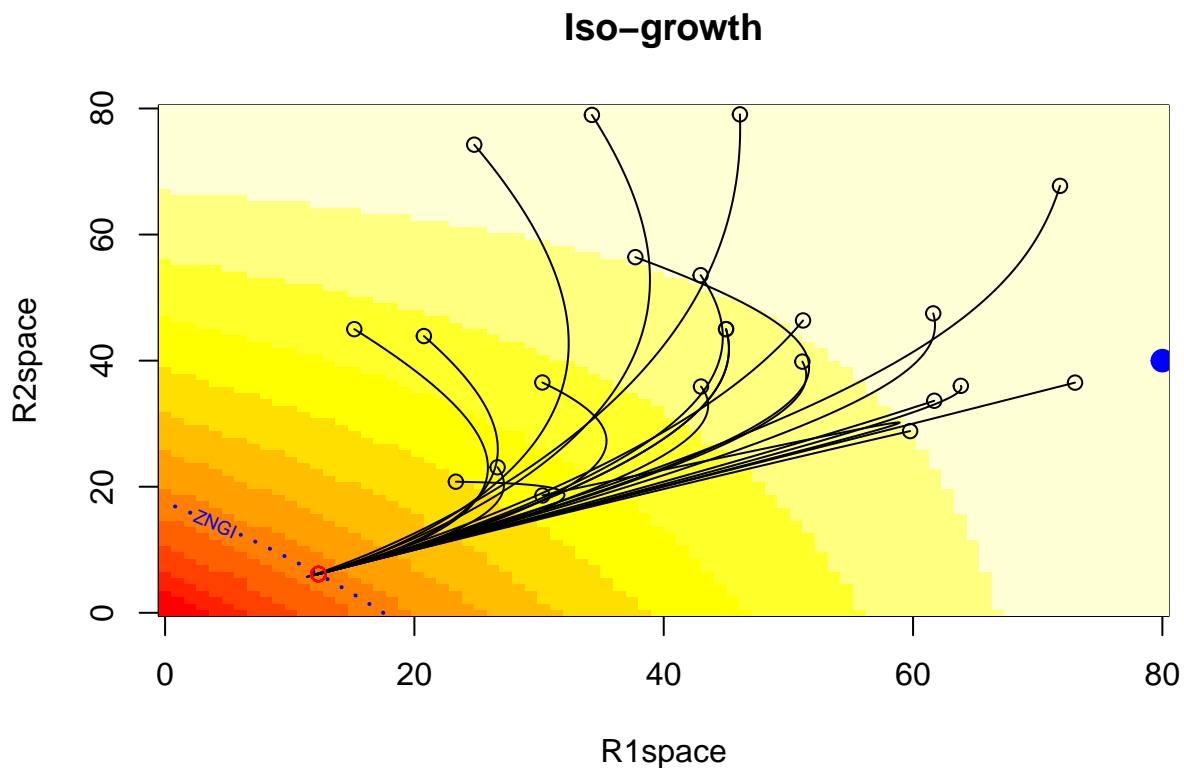
```

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

# define the perturbation of initial conditions in the matrix parRange
# nr and nc are number of rows and columns,
# next vector the values (of min and max)
# dimnames give names to columns and rows of the matrix
parRange <- matrix(nr = 3, nc = 2,
                  c(0.2, 10,10,50,80,80),
                  dimnames = list(c("N1_0","R1_0","R2_0"), c("min", "max")))

# calling fCRL for 20 set of parameters whitin the range parRange
CRL<-modCRL(fCRL,parRange=parRange,num = 20)

```



Exercise :

The objective is to see how the supply of ressources determines the equilibrium points and the size of population at equilibrium. So, instead of perturbing the initial conditions, we'll perturbate the position of the supply point.

- Copy the last code chunk below
- Which parameters should be perturbed ? -> modify `parRange` accordingly.

Inside the function `fCRL` * Removes the line changing the initial condition. The `X0` global value will be used instead. * Copy the global parameter vector `pars` in a local perturbed parameter vector. * Replace the value of perturbed parameters by those received in argument * use this perturbed parameter vector

instead of the global `pars` when computing the model solution.

For the plot: * add a blue point for the perturbed supply point, give it a size that depends on the size of population at equilibrium (use `cex = "N_eq"/20`). * add a blue line between the supply point and the reached equilibrium

```
# Just reproduce the same plot as above
image(R1space ,R2space ,f1space,main="Iso-growth")
contour(R1space ,R2space ,f1space,levels=as.vector(pars["mN1"]),
        add=T,col="blue",lty = "dotted", labels="ZNGI",lwd=2)

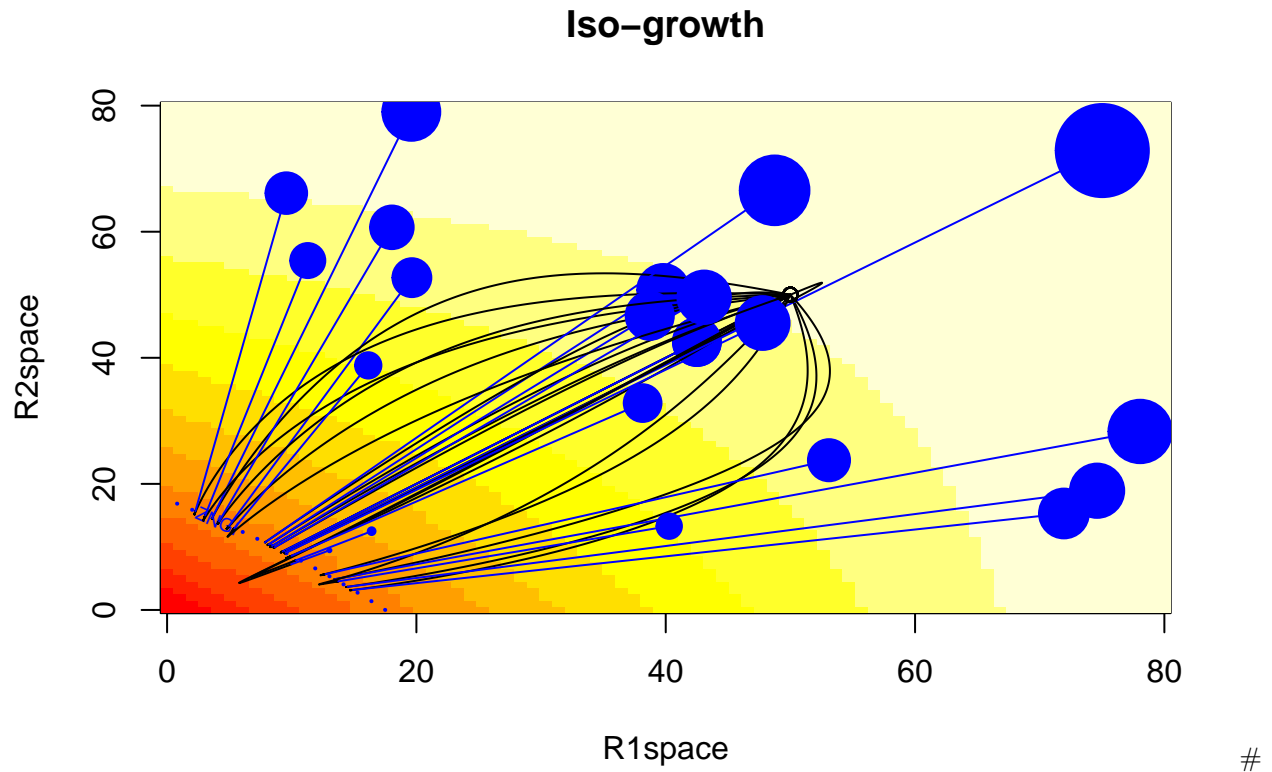
# define the function to be used by modCRL
fCRL<-function(parloc){
  perturbpars<-pars
  perturbpars[which(names(pars)%in%names(parloc))]<-parloc
  out<- ode(y = X0, times = times, func = simpleg, parms = perturbpars,method="euler")
  colnames(out)<-c("time", "N1", "R1", "R2")

  lines(out[, "R1"],out[, "R2"] )
  points(out[1, "R1"],out[1, "R2"])
  # points(out[nrow(out), "R1"],out[nrow(out), "R2"],col='green',pch=21,)
  points(perturbpars["g1"],perturbpars["g2"],col='blue',bg='blue',pch=21,cex=out[nrow(out), "N1"]/20 )
  lines(c(perturbpars["g1"],out[nrow(out), "R1"]),c(perturbpars["g2"],out[nrow(out), "R2"]) ,col='blue'

  return(c("R1eq"=out[nrow(out), "R1"], "R2eq"=out[nrow(out), "R2"]))
}

# define the perturbation of Ressource Supply Point in the matrix parRange
# nr and nc are number of rows and columns,
# next vector the values (of min and max)
# dimnames give names to columns and rows of the matrix
parRange <- matrix(nr = 2, nc = 2,
                   c(5,5,80,80),
                   dimnames = list(c("g1", "g2"), c("min", "max")))

# calling fCRL for 20 set of parameters within the range parRange
CRL<-modCRL(fCRL,parRange=parRange,num = 20)
```



Next

Next we will see what happens when two species competes for the same resources : [the 2 species case](#)

References

Soetaert, Karline, and Thomas Petzoldt. 2010. "Inverse modelling, sensitivity and monte carlo analysis in R using package FME." *Journal of Statistical Software* 33 (3): 1–28.

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