

Plant Coexistence and Herbivory

Exercises Accompanying the Course Environmental Modelling

Dries Bonte and Karline Soetaert, Ghent University

July 2021

Problem formulation

In wetlands, grasses and unpalatable plant species like *Iris* coexist. *Iris* grows slower but is competitively superior, with a logistic population growth only dependent on its own density. In contrast, the growth rates of the competitively inferior grasses are logistically determined by the combined biomass of grasses + *iris*.

Herbivores only consume grasses, but their consumption rate slows down when *Iris* is present. This is because the herbivores spend more energy to pick the grasses growing between the *Iris* plants.

Your task is to make a model that describes the interactions between grasses, *iris* and herbivores.

Assumptions

The following assumptions are made:

- Use a carrying capacity formulation to restrict the growth of both grasses and *iris*.
- Use the Monod-type functional response for grazing.
 - The half-saturation coefficient for grazing in the absence of *Iris* is ks .
 - Herbivore grazing is inhibited by an increasing *Iris* biomass. The strength of this inhibition is modeled with an exponential function, determined by the parameter *inhibct* (default 0).
- 35% of the consumed biomass is accumulated into herbivore body mass.

Use the following starting values (all in g dry biomass m^{-2}):

```
state <- c(GRASS = 50, IRIS = 2, HERB = 0.2) # g/m2
```

The following parameter settings are typical for a temperate grassland:

```
parms <- c(
  ktot    = 200, # [g/m2] carrying capacity of grass and unpalatable Iris
  assEff  = 0.35, # [-] efficiency at which cattle incorporate biomass into body mass
  ks      = 50, # [g/m2] half-saturation constant for functional response of grazing on grass
  rGraz   = 0.17, # [/d] grazing rate constant of herbivores
  rGrowG  = 0.05, # [/d] growth rate constant grass
  rGrowI  = 0.04, # [/d] growth rate constant Iris
  rResp   = 0.018, # [/d] basal metabolic rate constant
  inhibct = 0 # [/(g/m2)] strength of inhibition by Iris
)
```

Tasks

1. Use the above information to create the model and run it for 10 years. In a first run remove the grazing dependency on the IRIS density. Is there coexistence possible with these parameter settings?
 2. What happens if you include inhibition of grazing by Iris? How does this affect coexistence?
 3. To further increase realism, assume that in addition to grasses being grazed upon by large herbivores, unpalatable IRIS species also have their enemies, and are attacked by below-ground nematodes (round worms). Such pathogenic nematodes are prevalent, and we assume their impact is second-order with respect to the biomass density of their host. The rate constant that determines this infection equals to $0.01 (g/m^2)^{-1}d^{-1}$.
 4. One final elaboration is that the herbivores can leave the area, whereas nematodes cannot. This emigration is a second-order process with respect to the herbivore density characterized by the rate constant $0.001 (g/m^2)^{-1}d^{-1}$.
- Implement this model in *R*. You can start with the R-markdown template model file *RTM_0D.Rmd*.¹
 - Plot the model output.
 - Under which conditions do you find temporal coexistence for these competing species?

If you have time

- What happens if nematode virulence is decreasing due to local adaptation (trading off with *r*)?
- What happens if herbivore emigration rates are conditional on the iris density?

Answers

It is most efficient to create a model that can answer all questions at once. We do this by adding a number of extra parameters:

- *rEmigration*, the herbivore emigration rate constant, set to 0 if there is no emigration (default).
- *rInfect*, the nematode infection rate constant, set to 0 if there is no infection (default).

R implementation

```
require(deSolve) # package with solution methods

# state variables, Units: g/m2
state <- c(GRASS = 50, IRIS = 2, HERB = 0.2)

# parameters
parms <- c(
  ktot      = 200,    # [g/m2] carrying capacity of grass and unpalatable Iris
  assEff     = 0.35,  # [-] efficiency at which cattle incorporate biomass into body mass
  ks         = 50,    # [g/m2] half-saturation constant for functional response of grazing on grass
  rGraz      = 0.17,  # [/d] grazing rate constant of herbivores
  rGrowG     = 0.05,  # [/d] growth rate constant grass
  rGrowI     = 0.04,  # [/d] growth rate constant Iris
  rResp      = 0.018, # [/d] basal metabolic rate constant
  rEmigration = 0,    # [/d] emigration rate constant
  rInfect    = 0,    # [/(g/m2)/d] nematode infection rate constant
```

¹You can obtain this file from Rstudio: File → new File → Rmarkdown → from template → RTM_0D. Save this file under a different name, and do not forget to change the heading of this file.

```

    inhibct      = 0          # [/(g/m2)] strength of inhibition by Iris
  )

# Model function
GrassLand <- function(t, state, params) {
  with (as.list(c(state, params)), {

    # Rate expressions [g/m2/d]
    TotBiom      <- GRASS+IRIS

    # plants
    GrassGrowth <- rGrowG * GRASS * (1-(TotBiom/ktot))
    IrisGrowth  <- rGrowI * IRIS * (1-(IRIS /ktot))
    Infection    <- rInfect *IRIS*IRIS

    # herbivores
    Grazing      <- rGraz * HERB * GRASS/(GRASS+ks) *exp(-inhibct*IRIS)
    Emigration    <- rEmigration * HERB*HERB  #(density dependence)
    BasalResp     <- rResp * HERB

    # Mass balances [g/m2/d]
    dGRASS        <- GrassGrowth - Grazing
    dIRIS          <- IrisGrowth - Infection
    dHERB          <- assEff*Grazing - Emigration - BasalResp

    list( c(dGRASS, dIRIS, dHERB),
           total = TotBiom)
  })
}

```

Now we solve the model for various conditions: first the default run, then a run with IRIS-dependent grazing, with nematode infection, and finally two runs with emigration. We plot all results in one figure.

```

# output time
outtimes <- seq(from = 0, to = 3650, length.out = 1000)

# solve this model, using the ode function from deSolve
out <- ode(y = state, parms = parms, func = GrassLand, times = outtimes)

# iris-dependen grazing
parms2 <- parms
parms2["inhibct"] <- 1
out2 <- ode(y = state, parms = parms2, func = GrassLand, times = outtimes)

# Nematode infection
parms3 <- parms2
parms3["rInfect"] <- 0.001
out3 <- ode(y = state, parms = parms3, func = GrassLand, times = outtimes)

# Emigration
parms4 <- parms3
parms4["rEmigration"] <- 0.0001
out4 <- ode(y = state, parms = parms4, func = GrassLand, times = outtimes)

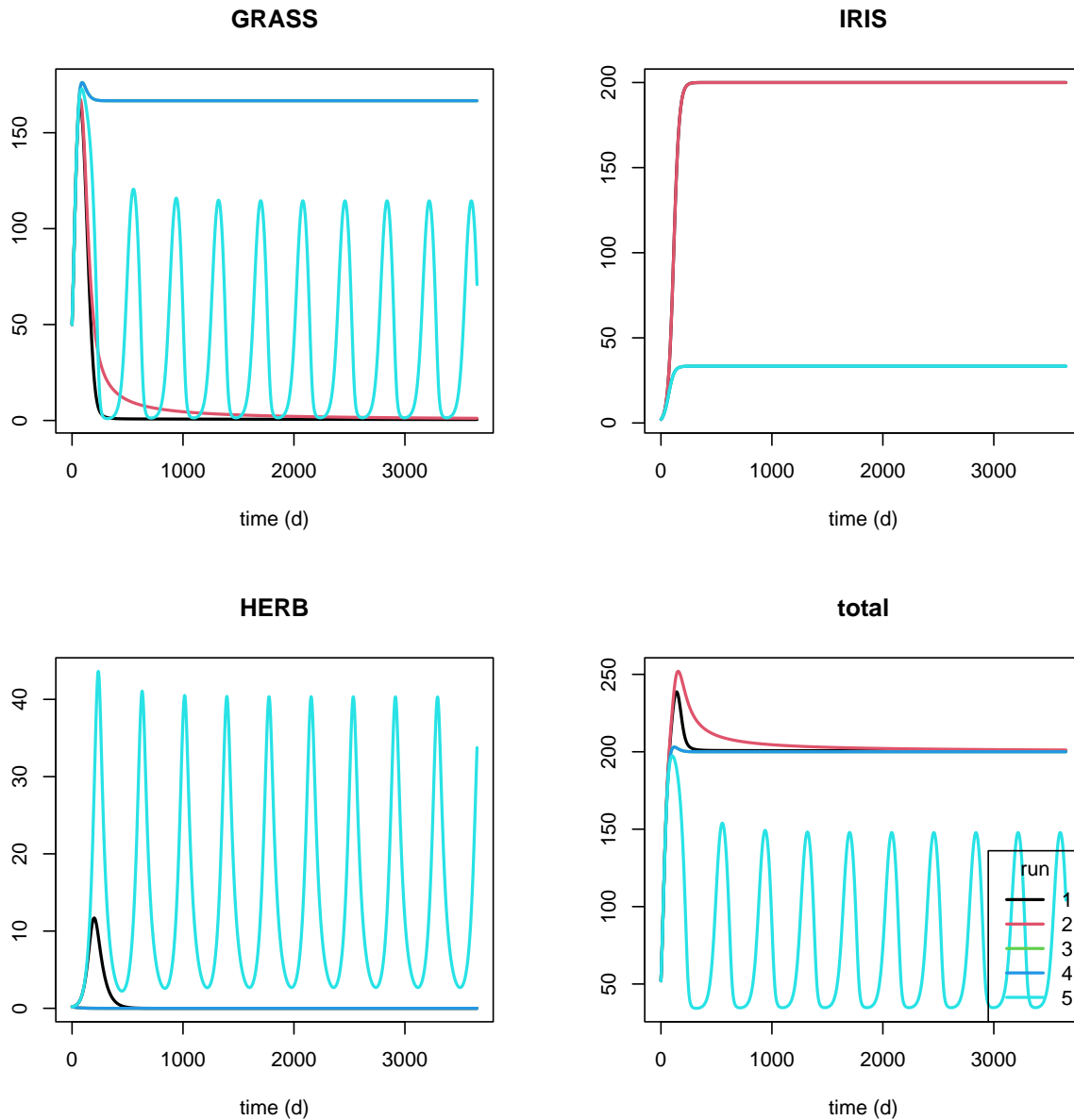
```

```

# Emigration + infection, but no inhibition of grazing by Iris
parms5 <- parms4
parms5["inhibct"] <- 0
out5 <- ode(y = state, parms = parms5, func = GrassLand, times = outtimes)

# plot all at once
plot(out, out2, out3, out4, out5, type = "l", lwd = 2, lty = 1, xlab="time (d)")
legend("bottomright", legend = 1:5, title = "run",
      col = 1:5, lwd = 2, lty = 1)

```



References

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Karline Soetaert, Thomas Petzoldt, R. Woodrow Setzer (2010). Solving Differential Equations in R: Package deSolve. *Journal of Statistical Software*, 33(9), 1–25. URL <http://www.jstatsoft.org/v33/i09/> DOI 10.18637/jss.v033.i09