Plant Coexistence and Herbivory

Exercises Accompanying the Course Environmental Modelling

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Problem formulation

In wetlands, grasses and unpalatable plant species like *Iris* coexist. Iris grows slower but is competitively superior, with logistic population growth only dependent on its own density. For the competitive inferior grasses in contrast, the growth rates 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 then spend more energy to pick the grasses in between the Iris plants.

You are to make a model that descibes 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 Monod-type of functional response for grazing.
  - The half-saturation coefficient for grazing in the absence of Iris is determined by a coefficient ks
  - Herbivore grazing is inhibited by increasing Iris biomasses. 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 wt which cattle incorporate biomass in body reserves
  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, now assume that, whereas grasses are attacked by large herbivores, unpalatable IRIS species also have their enemies, and are attacked by belowground nematodes (round worms). Such pathogenic nematodes are omniprevalent, and we assume their impact to increase quadratically with the presence of their host. The parameter that determines this infection equals 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 quadratically density-dependent process with a fixed emigration rate constant equal to 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* \footnote{you can download this file from Rstudio: "File->new File->Rmarkdown..->from template->RTM_0D". Save this file under a different name, do not forget to change the heading of this file.}.

- Plot its output. Discuss - 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, 0 in case there is no emigration (the default)
- rInfect, the nematode infection rate constant, set to 0 in the absence of infection

R implementation

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

```
## Loading required package: deSolve
```

```
# 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 wt which cattle incorporate biomass in body reserves
  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
```

```r
    rResp       = 0.018,  # [/d] basal metabolic rate constant
    rEmigration = 0,      # [/d] emigration rate constant
    rInfect     = 0,      # [/(g/m2)/d] nematode infection rate constant
    inhibct     = 0       # [/(g/m2)] strength of inhibition by Iris
)


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

# Model function
   # 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)
  })

}
```

We then 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 in one figure.

```r
# 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["nemInfect"] <- 0.001
out3 <- ode(y = state, parms = parms3, func = GrassLand, times = outtimes)
```

```r
# Emigration
parms4 <- parms3
parms4["emRate"] <- 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)
legend ("bottomright", legend = 1:5, title = "run",
        col = 1:5, lwd = 2, lty =1)
```
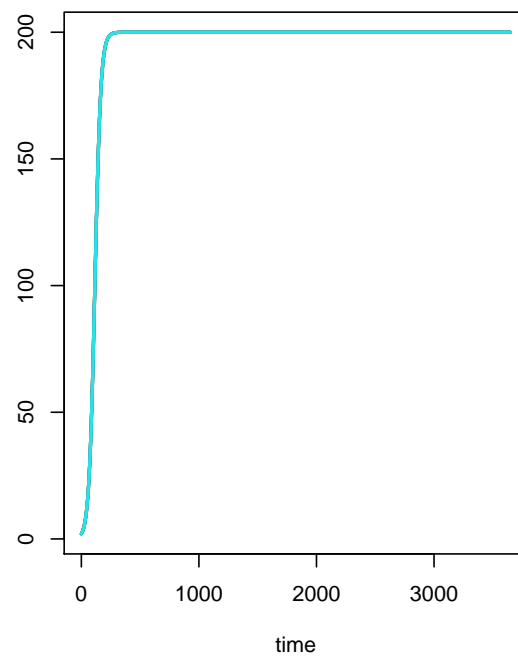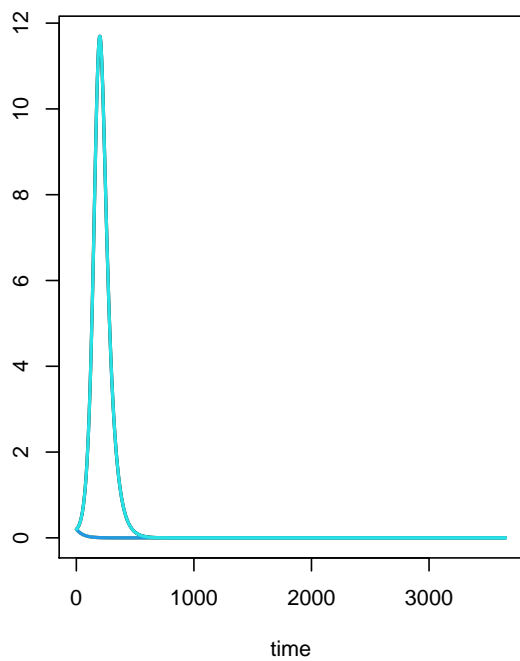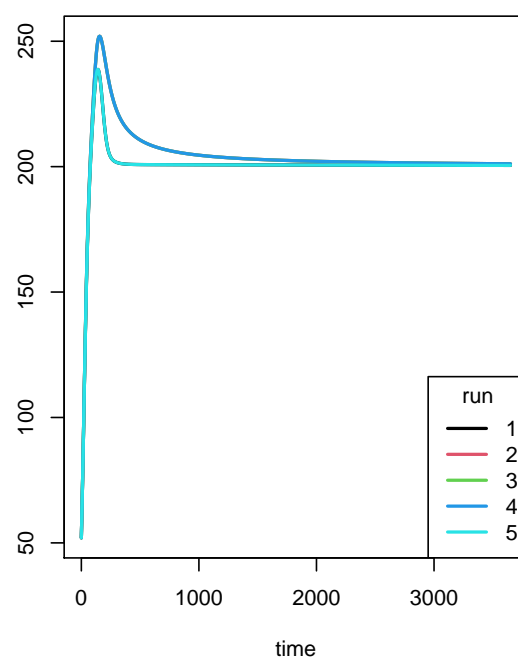
GRASS

IRIS

HERB

total

run
1
2
3
4
5

time

5
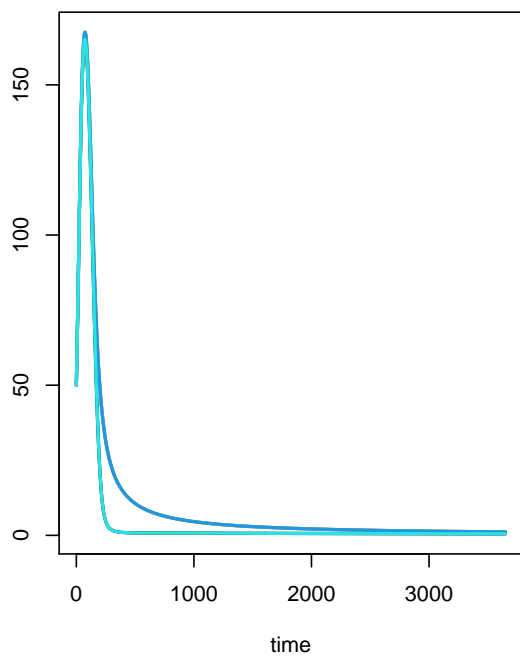
References

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