

microstegium-elymus-model-summary

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Summary

Simulation of *Microstegium vimineum* and *Elymus virginicus* over time. *M. vimineum* is an invasive annual grass and *E. virginicus* is a native perennial grass. *E. virginicus* grows by itself for 100 years, and then *M. vimineum* is introduced. Disease effects arise 100 years later. Population dynamics are similar in the absence of disease and when both species are susceptible to disease. In both cases, *M. vimineum* reduces the size of the *E. virginicus* population. *M. vimineum* is able to recover population losses due to disease. *E. virginicus* seedlings are impacted more than adults. When only *M. vimineum* is susceptible to disease, its population crashes.

Set-up

```
# clear all existing data
rm(list = ls())

# open libraries
library(data.table)
library(plotly)
library(cowplot)
library(popbio)
library(tidyverse)

# plotting parameters
axisText = 10
axisTitle = 12
legendText = 10
legendTitle = 0

# import data
params <- read_csv("../data/mv_ev_model_parameters_101519.csv", col_types = cols())
aparams <- read_csv("../data/mv_ev_model_alt_parameters_101519.csv", col_types = cols())
```

Parameters

Formatting:

- subscripts follow “.”
- p = perennial adult (at least 1 year old)
- s = perennial seedling (germinated that spring)
- a = annual
- L = annual litter

Edit:

```

# derive related parameters
dparams <- tibble(
  parameter = c("annual-adult competition",
                "seedling-adult competition",
                "adult-annual competition",
                "adult-seedling competition",
                "adult-adult competition",
                "seedling seed production"),
  symbol = c("alpha.pa",
             "alpha.ps",
             "alpha.ap",
             "alpha.sp",
             "alpha.pp",
             "lambda.s"),
  value = c(filter(params, symbol == "alpha.sa")$value/10,
            filter(params, symbol == "alpha.sa")$value/10,
            filter(params, symbol == "alpha.as")$value*10,
            filter(params, symbol == "alpha.as")$value*10,
            filter(params, symbol == "alpha.as")$value*10,
            filter(params, symbol == "lambda.p")$value/10)
) %>%
  mutate(units = c(rep("year-1", 5), "seeds year-1"),
         reference = "derived")

# merge with main parameters
params2 <- full_join(params,
                    dparams,
                    by = c("parameter", "symbol", "value", "units", "reference"))

# simulation time
years = 500

```

Table 1: Model parameter values

parameter	symbol	value	units	reference
perennial adult survival	m.p	0.9500	year ⁻¹	Malmstrom et al. 2005
annual seed survival	s.a	0.7400	year ⁻¹	Huebner 2011
perennial seed survival	s.s	0.7600	year ⁻¹	Robocker et al. 1953
annual germination	gamma.a	0.7000	year ⁻¹	Warren et al. 2013
perennial germination	gamma.s	0.6600	year ⁻¹	Robocker et al. 1953
litter suppression of annual germination	alpha.aL	-0.0009	g ⁻¹ year ⁻¹	Foster and Gross 1998
litter suppression of perennial germination	alpha.sL	-0.0009	g ⁻¹ year ⁻¹	Foster and Gross 1998
litter decomposition rate	b	0.5600	year ⁻¹	Kourtev et al. 2002
annual summer survival	h.a	0.9500	year ⁻¹	Warren et al. 2013
perennial seedlingsummer survival	h.s	0.4000	year ⁻¹	Mottl et al. 2006
perennial adult summer survival	h.p	0.8300	year ⁻¹	Mottl et al. 2006
annual seed production	lambda.a	6500.0000	seeds year ⁻¹	Wilson et al. 2015
perennial seed production	lambda.p	435.0000	seeds year ⁻¹	Stevens 1957
annual-annual competition	alpha.aa	0.1220	year ⁻¹	Leicht et al. 2005
seedling-annual competition	alpha.as	0.3570	year ⁻¹	Leicht et al. 2005
seedling-seedling competition	alpha.ss	0.0020	year ⁻¹	Leicht et al. 2005
annual-seedling competition	alpha.sa	0.7240	year ⁻¹	Leicht et al. 2005
biomass-seed conversion	c.a	0.0050	g seeds ⁻¹ year ⁻¹	Wilson et al. 2015

parameter	symbol	value	units	reference
disease suppression of annual seed production	tol.a	0.1900	year ⁻¹	Flory et al. 2011
disease suppression of perennial seed production	tol.p	0.1900	year ⁻¹	Flory et al. 2011
annual-adult competition	alpha.pa	0.0724	year ⁻¹	derived
seedling-adult competition	alpha.ps	0.0724	year ⁻¹	derived
adult-annual competition	alpha.ap	3.5700	year ⁻¹	derived
adult-seedling competition	alpha.sp	3.5700	year ⁻¹	derived
adult-adult competition	alpha.pp	3.5700	year ⁻¹	derived
seedling seed production	lambda.s	43.5000	seeds year ⁻¹	derived

Table 2: Alternative model parameter values

parameter	symbol	value	units	reference
annual germination	gamma.a	0.29	year ⁻¹	Huebner 2011
annual intraspecific seed competition	alpha.aa	0.001, 0.015, 0.054	year ⁻¹	Leicht et al. 2005
annual interspecific competition	alpha.as	0.054, 0.910, 17.919	year ⁻¹	Leicht et al. 2005
perennial intraspecific competition	alpha.ss	0.006, 0.011, 0.049	year ⁻¹	Leicht et al. 2005
perennial interspecific seed competition	alpha.sa	1.347, 9.574, 23.070	year ⁻¹	Leicht et al. 2005
disease suppression of seed production	tol	0.6	year ⁻¹	Stricker et al. 2016

Model

Population equations:

Assume counts are being conducted in the fall

$$N.s[t+1] = s.s * (1-g.s) * N.s[t] + g.s * h.s * f.s * N.s[t] + m.p * f.p * N.p[t]$$

perennial seeds = seed bank survival + seedling seed production + adult seed production

$$N.p[t+1] = m.p * N.p[t] + g.s * h.s * N.s[t]$$

perennial adults = survival + seedling maturation

$$N.a[t+1] = s.a * (1-g.a) * N.a[t] + g.a * h.a * f.a * N.a[t]$$

annual seeds = seed bank survival + seed production

$$L[t+1] = b * c.a * g.a * h.a * f.a * N.a[t-1] + b * L[t]$$

annual litter = biomass from previous fall + decomposition

Density-dependence on fecundity

$$f.s = lam.s / (1 + alpha.ss * g.s * h.s * N.s[t] + alpha.sp * m.p * N.p[t] + alpha.sa * g.a * h.a * N.a[t])$$

perennial seedling fecundity = fecundity in the absence of competition / (perennial seedling competition + perennial adult competition + annual competition)

$$f.p = lam.p / (1 + alpha.ps * g.s * h.s * N.s[t] + alpha.pp * m.p * N.p[t] + alpha.pa * g.a * h.a * N.a[t])$$

perennial adult fecundity = fecundity in the absence of competition / (perennial seedling competition + perennial adult competition + annual competition)

$$f.a = lam.a / (1 + alpha.as * g.s * h.s * N.s[t] + alpha.ap * m.p * N.p[t] + alpha.aa * g.a * h.a * N.a[t])$$

annual fecundity = fecundity in the absence of competition / (perennial seedling competition + perennial adult competition + annual competition)

Litter suppression

$g.s = \text{gamma.s} + (\text{alpha.sL} * L[t])$

perennial seed germination = germination in the absence of litter + reduction due to litter ($\text{alpha.sL} < 0$, $g.s$ constrained to ≥ 0)

$g.a = \text{gamma.a} + (\text{alpha.aL} * L[t])$

annual seed germination = germination in the absence of litter + reduction due to litter ($\text{alpha.aL} < 0$, $g.a$ constrained to ≥ 0)

Function

```
simFun = function(params, NO.a, NO.s, NO.p, L0, Ni.a, simtime) {  
  
  # define parameters  
  m.p = filter(params, symbol == "m.p")$value  
  s.a = filter(params, symbol == "s.a")$value  
  s.s = filter(params, symbol == "s.s")$value  
  gamma.a = filter(params, symbol == "gamma.a")$value  
  gamma.s = filter(params, symbol == "gamma.s")$value  
  alpha.aL = filter(params, symbol == "alpha.aL")$value  
  alpha.sL = filter(params, symbol == "alpha.sL")$value  
  b = filter(params, symbol == "b")$value  
  h.a = filter(params, symbol == "h.a")$value  
  h.s = filter(params, symbol == "h.s")$value  
  h.p = filter(params, symbol == "h.p")$value  
  lambda.a = filter(params, symbol == "lambda.a")$value  
  lambda.p = filter(params, symbol == "lambda.p")$value  
  lambda.s = filter(params, symbol == "lambda.s")$value  
  alpha.aa = filter(params, symbol == "alpha.aa")$value  
  alpha.as = filter(params, symbol == "alpha.as")$value  
  alpha.ap = filter(params, symbol == "alpha.ap")$value  
  alpha.sa = filter(params, symbol == "alpha.sa")$value  
  alpha.ss = filter(params, symbol == "alpha.ss")$value  
  alpha.sp = filter(params, symbol == "alpha.sp")$value  
  alpha.pa = filter(params, symbol == "alpha.pa")$value  
  alpha.ps = filter(params, symbol == "alpha.ps")$value  
  alpha.pp = filter(params, symbol == "alpha.pp")$value  
  c.a = filter(params, symbol == "c.a")$value  
  tol.a = filter(params, symbol == "tol.a")$value  
  tol.p = filter(params, symbol == "tol.p")$value  
  
  # initialize populations  
  N.a = rep(NA, simtime)  
  N.s = rep(NA, simtime)  
  N.p = rep(NA, simtime)  
  L = rep(NA, simtime)  
  
  N.a[1] = NO.a  
  N.s[1] = NO.s  
  N.p[1] = NO.p  
  L[1] = L0  
  
  # simulate population dynamics  
  for (t in 1:(simtime - 1)) {
```

```

# introduce annual at t=100
N.a[t] = ifelse(N0.a == 0 & t == 100, Ni.a, N.a[t])

# calculate parameters to introduce disease at t=200
lam.a = ifelse(t < 200, lambda.a, tol.a * lambda.a)
lam.p = ifelse(t < 200, lambda.p, tol.p * lambda.p)
lam.s = ifelse(t < 200, lambda.s, tol.p * lambda.s)

# reduce germination due to litter
g.s = gamma.s + (alpha.sL * L[t])
g.s = ifelse(g.s < 0, 0, g.s)
g.a = gamma.a + (alpha.aL * L[t])
g.a = ifelse(g.a < 0, 0, g.a)

# reduce fecundity due to competition
f.s = lam.s / (1 + alpha.ss * g.s * h.s * N.s[t] + alpha.sp * m.p *
  N.p[t] + alpha.sa * g.a * h.a * N.a[t])
f.p = lam.p / (1 + alpha.ps * g.s * h.s * N.s[t] + alpha.pp * m.p *
  N.p[t] + alpha.pa * g.a * h.a * N.a[t])
f.a = lam.a / (1 + alpha.as * g.s * h.s * N.s[t] + alpha.ap * m.p *
  N.p[t] + alpha.aa * g.a * h.a * N.a[t])

# population size
N.s[t + 1] = s.s * (1 - g.s) * N.s[t] + g.s * h.s * f.s * N.s[t] +
  m.p * f.p * N.p[t]
N.p[t + 1] = m.p * N.p[t] + g.s * h.s * N.s[t]
N.a[t + 1] = s.a * (1 - g.a) * N.a[t] + g.a * h.a * f.a * N.a[t]
L[t + 1] = ifelse(t > 2, b * c.a * g.a * h.a * f.a * N.a[t - 1] +
  b * L[t], L0)

# correct to prevent negative numbers
N.s[t + 1] = ifelse(N.s[t + 1] < 1, 0, N.s[t + 1])
N.p[t + 1] = ifelse(N.p[t + 1] < 1, 0, N.p[t + 1])
N.a[t + 1] = ifelse(N.a[t + 1] < 1, 0, N.a[t + 1])
L[t + 1] = ifelse(L[t + 1] < 0, 0, L[t + 1])
}

# save data
dfN = data.frame(time = rep(1:simtime, 4), N = c(N.s, N.p, N.a, L),
  species = rep(c("Elymus seedling", "Elymus adult", "Microstegium",
    "Microstegium litter"), each = simtime))

# return
return(dfN)
}

```

Simulations

Default parameters

```

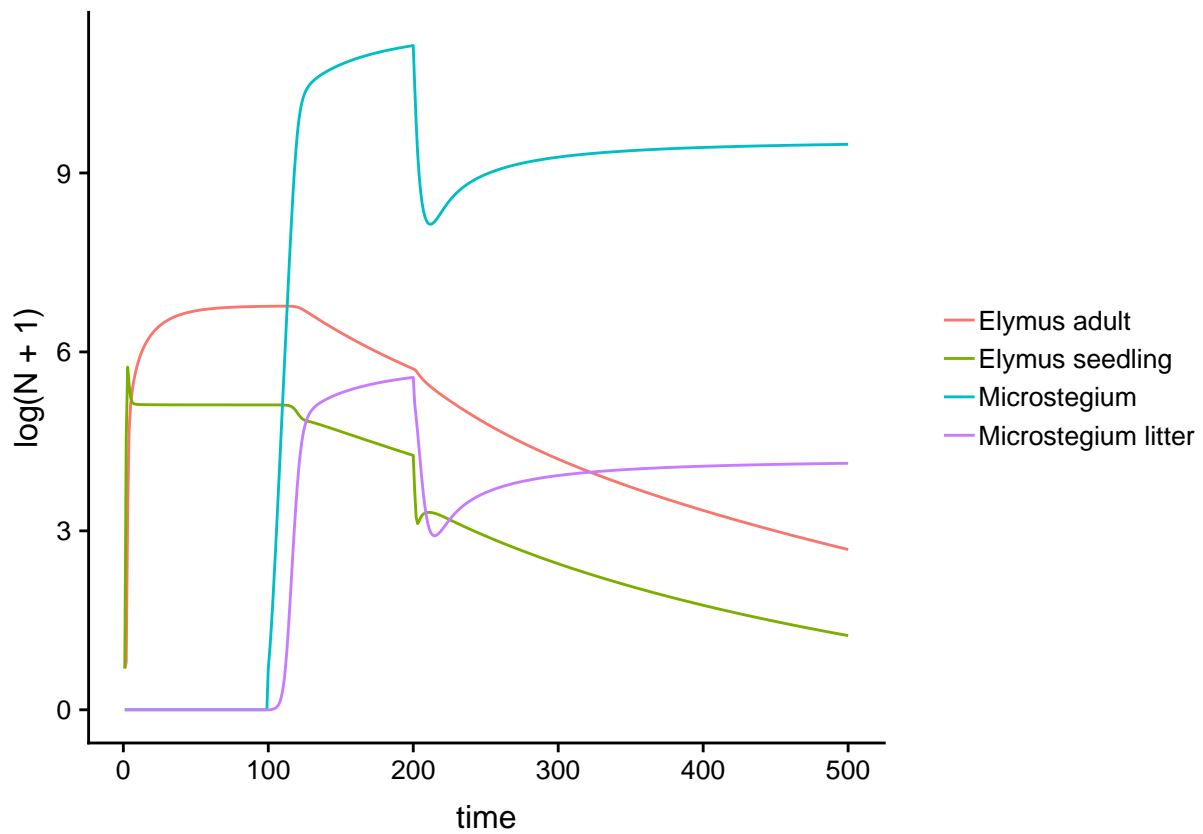
simFun(params = params2,
  N0.a = 0,

```

```

NO.s = 1,
NO.p = 1,
LO = 0,
Ni.a = 1,
simtime=years) %>%
ggplot(aes(x = time, y = log(N+1), color = species)) +
geom_line() +
theme(axis.text = element_text(size = axisText),
      axis.title = element_text(size = axisTitle),
      legend.text = element_text(size = legendText),
      legend.title = element_text(size = legendTitle))

```



Remove disease

```

simFun(params = params2 %>% mutate(value = case_when(symbol %in% c("tol.a", "tol.p") ~ 1,
                                                         TRUE ~ value)),

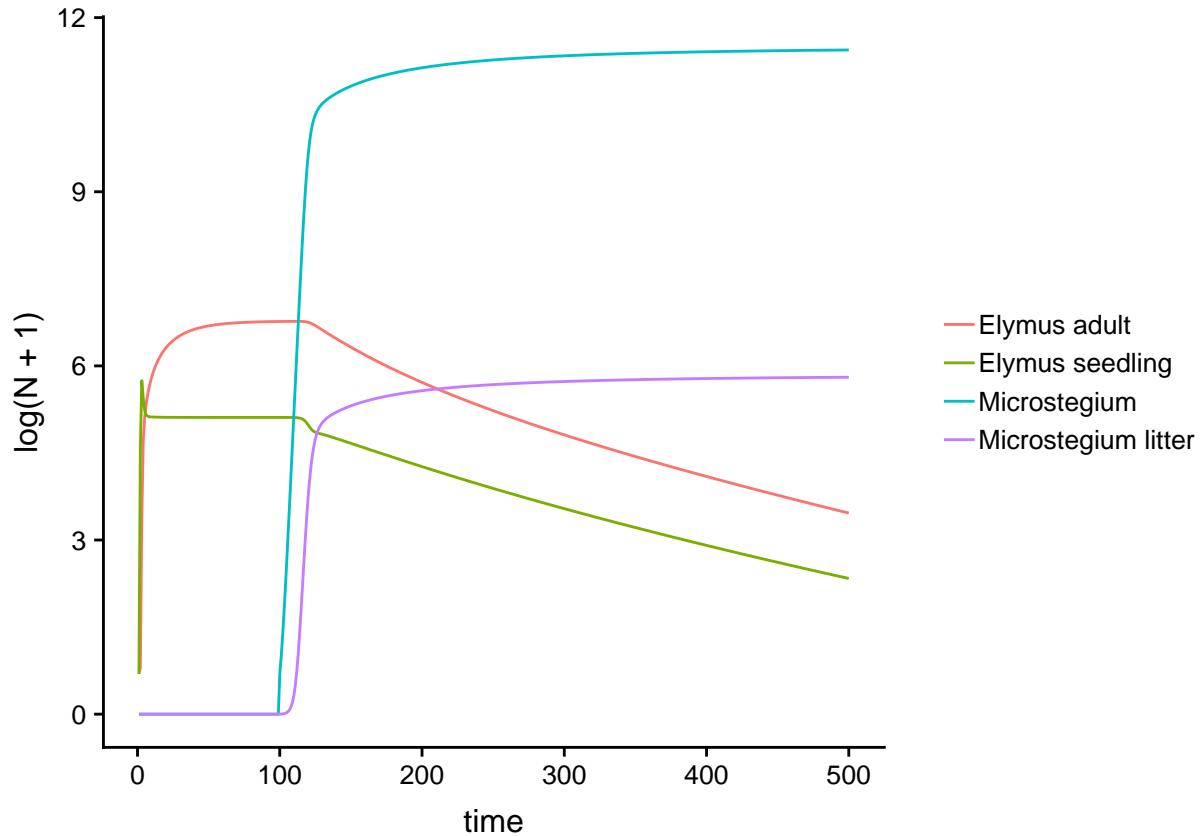
        NO.a = 0,
        NO.s = 1,
        NO.p = 1,
        LO = 0,
        Ni.a = 1,
        simtime=years) %>%
ggplot(aes(x = time, y = log(N+1), color = species)) +
geom_line() +

```

```

theme(axis.text = element_text(size = axisText),
      axis.title = element_text(size = axisTitle),
      legend.text = element_text(size = legendText),
      legend.title = element_text(size = legendTitle))

```



Remove disease from perennial

```

simFun(params = params2 %>% mutate(value = case_when(symbol == "tol.p" ~ 1,
                                                       TRUE ~ value)),

      NO.a = 0,
      NO.s = 1,
      NO.p = 1,
      LO = 0,
      Ni.a = 1,
      simtime=years) %>%
ggplot(aes(x = time, y = log(N+1), color = species)) +
geom_line() +
theme(axis.text = element_text(size = axisText),
      axis.title = element_text(size = axisTitle),
      legend.text = element_text(size = legendText),
      legend.title = element_text(size = legendTitle))

```

