

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_102119.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 | 0.5800 | 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

$$L[t+1] = c.a * g.a * h.a * N.a[t] + L[t] * e^{-b}$$

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] = c.a * g.a * h.a * N.a[t] + L[t] * exp(-b)

# 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

```

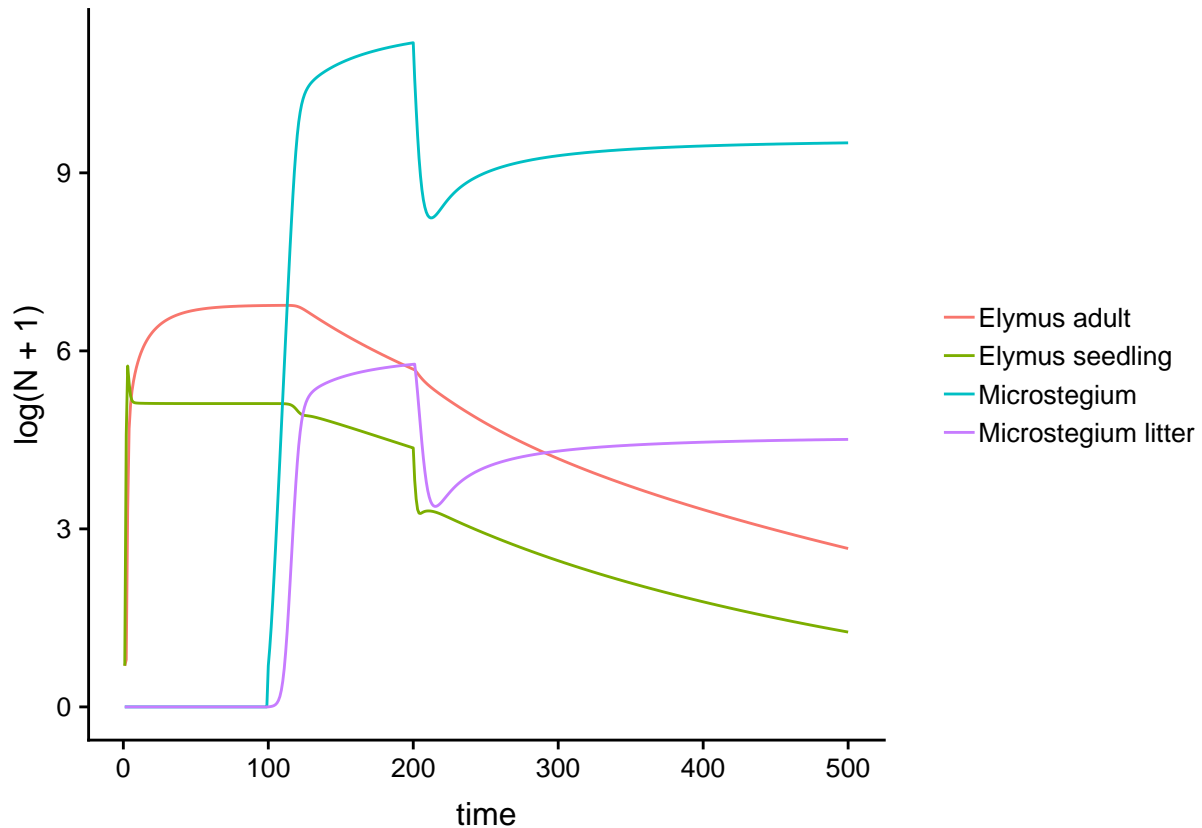
simFun(params = params2,
  N0.a = 0,
  N0.s = 1,

```

```

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 both species

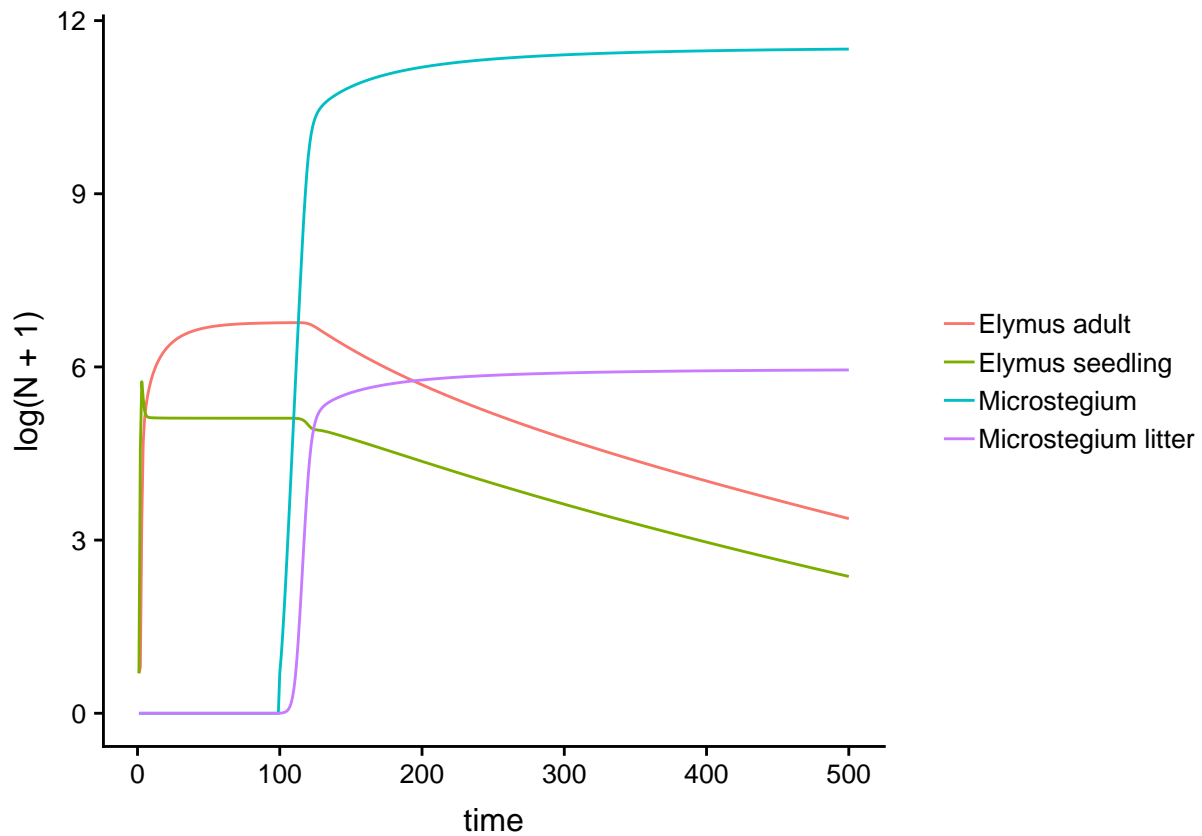
```

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))
```

