microstegium_elymus_model_summary

Amy Kendig

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Contents

1	Summary	1
2	Set-up	2
3	Parameters 3.1 Formatting	2 2 2 3 3
4	Model4.1 Population equations	4 4 4 5
5	Function	5
6	Simulations 6.1 No disease, Microstegium by itself 6.2 No disease, Microstegium invades Elymus 6.3 No disease, co-introduced 6.4 Disease, Microstegium by itself 6.5 Disease, Microstegium invades Elymus 6.6 Disease, co-introduced 6.7 No disease, Elymus by itself 6.8 No disease, Elymus invades Microstegium 6.9 Disease, Elymus by itself 6.10 Disease, Elymus invades Microstegium	6 6 7 8 9 10 11 12 13 14 15
7	Population Figure	16

1 Summary

Simulation of *Microstegium vimineum* and *Elymus virgincus* over time. *M. vimineum* is an invasive annual grass and *E. virginicus* is a native perennial grass, with two stages: seedling and adult. Simulations are conducted for each species alone and invading the other after it has had time to establish (100 years). Simulations are also conducted in which both species are introduced to the system at the same time. In the absence of disease, *M. vimineum* is predicted to persist alone, but it is out-competed by *E. virginicus*. In the presence of disease, the competitive hierarchy reverses: *E. virginicus* can persist alone, but it is outcompeted

by *M. vimineum*. *Microstegium vimineum* experiences a net benefit from the presence of disease, likely due to lower intraspecific competition, even though its biomass production and survival are lower. *Elymus virgincus* also experiences losses in biomass and survival in the presence of disease, but intraspecific competition does not decrease. Results were consistent whether species invaded one another or were "co-introduced".

2 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
colPal = c("#0072B2", "#56B4E9", "#009E73", "#E69F00")
# import data
params <- read_csv("../data/mv_ev_model_parameters_experiment_072120.csv", col_types = cols())</pre>
params_dis <- read_csv(".../data/mv_ev_model_disease_parameters_experiment_072120.csv", col_types = cols
```

3 Parameters

3.1 Formatting

- subscripts follow "."
- A = annual plant
- L = annual litter
- P = perennial adult (at least 1 year old)
- S = perennial seedling (germinated that spring)
- Composite parameters are capitalized

3.2 Settings

```
# simulation time
simtime = 500

# invasion time
invtime = 100

# initial conditions
```

```
NO.A = 1 # initial annual population size

NO.S = 1 # initial perennial seedling population size

NO.P = 0 # initial perennial adult population size

LO = 0 # initial annual litter amount

Ni.A = 1 # introduction of annual

Ni.S = 1 # introduction of perennial
```

3.3 "No disease" parameters from experiments

parameter	symbol	value	units
annual germination without litter	g.A	0.6000	year ⁻¹
litter suppression of annual germination	beta.A	1.0300	$g^{-1} year^{-1}$
annual seed survival	s.A	0.1250	year ⁻¹
annual seedling survival	h.A	0.9800	year ⁻¹
annual biomass without competition	v.A	42.2300	g year ⁻¹
intraspecific effect of competition on annual	alpha.AA	0.1900	year ⁻¹
interspecific seedling effect of competition on annual	alpha.AS	0.1900	year ⁻¹
interspecific adult effect of competition on annual	alpha.AP	0.1300	year ⁻¹
annual biomass-seed conversion	y.A	30.7500	seeds g^{-1} year ⁻¹
annual litter-biomass conversion	a	1.0000	year ⁻¹
litter decomposition rate	b	0.6700	year ⁻¹
perennial germination without litter	g.S	0.4400	year ⁻¹
litter suppression of perennial germination	beta.S	0.0240	$g^{-1} year^{-1}$
perennial seed survival	s.S	0.1100	year ⁻¹
seedling perennial biomass without competition	v.S	2.0000	g year ⁻¹
adult perennial biomass without competition	v.P	8.4800	g year ⁻¹
intraspecific seedling effect of competition on perennial seedling	alpha.SS	0.0068	year ⁻¹
interspecific effect of competition on perennial seedling	alpha.SA	0.0140	year ⁻¹
intraspecific adult effect of competition on perennial seedling	alpha.SP	0.0470	year ⁻¹
intraspecific adult effect of competition on perennial adult	alpha.PP	0.0690	year ⁻¹
intraspecific seedling effect of competition on perennial adult	alpha.PS	0.1800	year ⁻¹
interspecific effect of competition on perennial adult	alpha.PA	0.0650	year ⁻¹
perennial seedling biomass-seed conversion	y.S	6.3200	seeds g^{-1} year ⁻¹
perennial adult biomass-seed conversion	y.P	18.4500	seeds g^{-1} year ⁻¹
perennial seedling summer survival	h.S	0.9800	year ⁻¹
perennial adult summer survival	h.P	0.9500	year ⁻¹
perennial seedling winter survival	w.S	0.9200	year ⁻¹
perennial adult winter survival	w.P	0.9800	year ⁻¹

3.4 "Disease" parameters from experiments

parameter	symbol	value	units
annual germination without litter	g.A	0.6000	year ⁻¹
litter suppression of annual germination	beta.A	1.0300	g ⁻¹ year ⁻¹
annual seed survival	s.A	0.1250	year ⁻¹
annual seedling survival	h.A	0.9500	year ⁻¹
annual biomass without competition	v.A	26.4700	g year ⁻¹
intraspecific effect of competition on annual	alpha.AA	0.0860	year ⁻¹
interspecific seedling effect of competition on annual	alpha.AS	0.0780	year ⁻¹

parameter	symbol	value	units
interspecific adult effect of competition on annual	alpha.AP	0.1300	year ⁻¹
annual biomass-seed conversion	y.A	33.7600	seeds g^{-1} year ⁻¹
annual litter-biomass conversion	a	1.0000	year ⁻¹
litter decomposition rate	b	0.6700	year ⁻¹
perennial germination without litter	g.S	0.4400	year ⁻¹
litter suppression of perennial germination	beta.S	0.0240	$g^{-1} year^{-1}$
perennial seed survival	s.S	0.1100	year ⁻¹
seedling perennial biomass without competition	v.S	1.5700	g year ⁻¹
adult perennial biomass without competition	v.P	6.8500	g year ⁻¹
intraspecific seedling effect of competition on perennial seedling	alpha.SS	0.0076	year ⁻¹
interspecific effect of competition on perennial seedling	alpha.SA	0.0110	year ⁻¹
intraspecific adult effect of competition on perennial seedling	alpha.SP	0.0580	year ⁻¹
intraspecific adult effect of competition on perennial adult	alpha.PP	0.2600	year ⁻¹
intraspecific seedling effect of competition on perennial adult	alpha.PS	0.0430	year ⁻¹
interspecific effect of competition on perennial adult	alpha.PA	0.0480	year ⁻¹
perennial seedling biomass-seed conversion	y.S	5.2700	seeds g^{-1} year ⁻¹
perennial adult biomass-seed conversion	y.P	15.4500	seeds g^{-1} year ⁻¹
perennial seedling summer survival	h.S	0.8900	year ⁻¹
perennial adult summer survival	h.P	0.8800	year ⁻¹
perennial seedling winter survival	w.S	0.9000	year ⁻¹
perennial adult winter survival	w.P	0.9800	year ⁻¹

4 Model

4.1 Population equations

Assume counts are being conducted in the spring

```
\begin{split} \text{N.A[t+1]} &= \text{s.A} * (\text{1-G.A}) * \text{N.A[t]} + \text{G.A} * \text{h.A} * \text{V.A} * \text{y.A} * \text{N.A[t]} \\ \text{annual seeds} &= \text{seed bank survival} + \text{seed production} \\ \text{L[t+1]} &= \text{a} * \text{G.A} * \text{h.A} * \text{V.A} * \text{N.A[t]} + (\text{1-b}) * \text{L[t]} \\ \text{annual litter} &= \text{biomass from previous fall} + \text{decomposition} \\ \text{N.S[t+1]} &= \text{s.S} * (\text{1-G.S}) * \text{N.S[t]} + \text{G.S} * \text{h.S} * \text{V.S} * \text{y.S} * \text{N.S[t]} + \text{h.P} * \text{V.P} * \text{y.P} * \text{N.P[t]} \\ \text{perennial seeds} &= \text{seed bank survival} + \text{seedling seed production} + \text{adult seed production} \\ \text{N.P[t+1]} &= \text{h.P} * \text{w.P} * \text{N.P[t]} + \text{G.S} * \text{h.S} * \text{w.S} * \text{N.S[t]} \\ \text{perennial adults} &= \text{survival} + \text{seedling maturation} \\ \end{split}
```

4.2 Litter suppression of germination

$$\begin{split} & G.A = g.A \ / \ (1 + beta.A * L[t]) \\ & annual \ seed \ germination = germination \ in \ the \ absence \ of \ litter \ / \ reduction \ due \ to \ litter \\ & G.S = g.S \ / \ (1 + beta.S * L[t]) \\ & perennial \ seed \ germination = germination \ in \ the \ absence \ of \ litter \ / \ reduction \ due \ to \ litter \end{split}$$

4.3 Density-dependence on growth and fecundity

 $V.A = v.A \ / \ (1 + alpha.AA * G.A * h.A * N.A[t] + alpha.AP * h.P * N.P[t] + alpha.AS * h.S * G.S * N.S[t])$

annual growth = growth in the absence of competition / (competition from annuals + competition from perennial adults + competition from perennial seedlings)

 $V.S = v.S \ / \ (1 + alpha.SA * G.A * h.A * N.A[t] + alpha.SP * h.P * N.P[t] + alpha.SS * h.S * G.S * N.S[t]) \\ perennial seedling growth = growth in the absence of competition / (competition from annuals + competition from perennial adults + competition from perennial seedlings)$

 $V.P = v.P \ / \ (1 + alpha.PA * G.A * h.A * N.A[t] + alpha.PP * h.P * N.P[t] + alpha.PS * h.S * G.S * N.S[t]) \\ perennial adult growth = growth in the absence of competition / (competition from annuals + competition from perennial adults + competition from perennial seedlings)$

5 Function

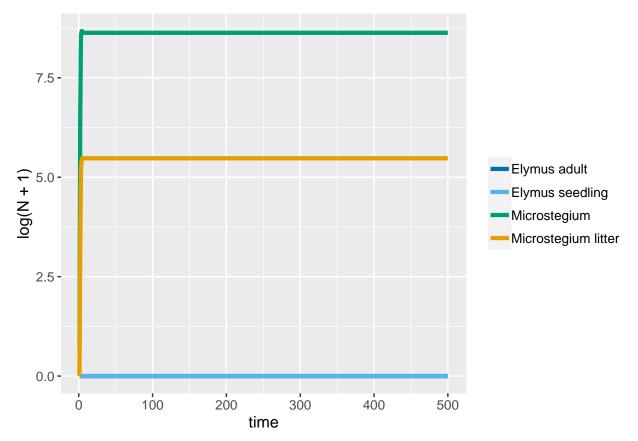
```
simFun = function(params, NO.A, NO.S, NO.P, LO, Ni.A, Ni.S, simtime, invtime, invader){
  # define parameters
  g.A = filter(params, symbol == "g.A")$value
  beta.A = filter(params, symbol == "beta.A")$value
  s.A = filter(params, symbol == "s.A")$value
  h.A = filter(params, symbol == "h.A")$value
  v.A = filter(params, symbol == "v.A")$value
  alpha.AA = filter(params, symbol == "alpha.AA")$value
  alpha.AS = filter(params, symbol == "alpha.AS")$value
  alpha.AP = filter(params, symbol == "alpha.AP")$value
  y.A = filter(params, symbol == "y.A")$value
  a = filter(params, symbol == "a")$value
  b = filter(params, symbol == "b")$value
  g.S = filter(params, symbol == "g.S")$value
  beta.S = filter(params, symbol == "beta.A")$value
  s.S = filter(params, symbol == "s.S")$value
  v.S = filter(params, symbol == "v.S")$value
  v.P = filter(params, symbol == "v.P")$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
  y.S = filter(params, symbol == "y.S")$value
  y.P = filter(params, symbol == "y.P")$value
  h.S = filter(params, symbol == "h.S")$value
  h.P = filter(params, symbol == "h.P")$value
  w.S = filter(params, symbol == "w.S")$value
  w.P = filter(params, symbol == "w.P")$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 invader
          N.A[t] = ifelse(t == invtime & invader == "annual", Ni.A, N.A[t])
          N.S[t] = ifelse(t == invtime & invader == "perennial", Ni.S, N.S[t])
          # reduce germination due to litter
          G.A = g.A / (1 + beta.A * L[t])
          G.S = g.S / (1 + beta.S * L[t])
          # reduce fecundity or growth due to competition
          V.A = v.A / (1 + alpha.AA * G.A * h.A * N.A[t] + alpha.AP * h.P * N.P[t] + alpha.AS * h.S * G.S * N.A[t] + alpha.AS * h.S * G.S * Alpha.AS * h.S * G.S * G.S * N.A[t] + alpha.AS * h.S * G.S * Alpha.AS * Alpha.AS * Alpha.AS * Alpha.AS * Alpha.AS * Alpha.
          V.S = v.S / (1 + alpha.SA * G.A * h.A * N.A[t] + alpha.SP * h.P * N.P[t] + alpha.SS * h.S * G.S * N.A[t] + alpha.SP * h.P * N.P[t] + alpha.SP * N.P[
          V.P = v.P / (1 + alpha.PA * G.A * h.A * N.A[t] + alpha.PP * h.P * N.P[t] + alpha.PS * h.S * G.S * N.P. + alpha.PS * h.S * G.S * G.S * N.P. + alpha.PS * G.S * G.S * N.P. + alpha.PS * G.S * G.
          # population size
          N.A[t+1] = s.A * (1-G.A) * N.A[t] + G.A * h.A * V.A * y.A * N.A[t]
          L[t+1] = a * G.A * h.A * V.A * N.A[t] + (1-b) * L[t]
          N.S[t+1] = s.S * (1-G.S) * N.S[t] + G.S * h.S * V.S * y.S * N.S[t] + h.P * V.P * y.P * N.P[t]
          N.P[t+1] = h.P * w.P * N.P[t] + G.S * h.S * w.S * N.S[t]
          # correct to prevent negative numbers
          N.A[t+1] = ifelse(N.A[t+1] < 1, 0, N.A[t+1])
          L[t+1] = ifelse(L[t+1] < 1, 0, L[t+1])
          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])
}
# save data
dfN = data.frame(time = rep(1:simtime, 4), N = c(N.S, N.P, N.A, L), species = rep(c("Elymus seedling"
# return
return(dfN)
```

6 Simulations

6.1 No disease, Microstegium by itself

```
# run simulation
no_dis_mv_alone_sim <- simFun(params, NO.A, NO.S = 0, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "none")
# figure of time series</pre>
```



6.2 No disease, Microstegium invades Elymus

```
legend.text = element_text(size = legendText),
legend.title = element_text(size = legendTitle)) +
scale_color_manual(values = colPal)
```

```
T.5-

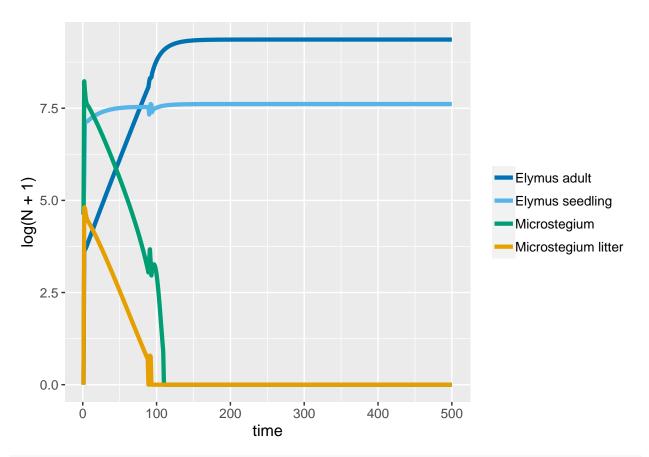
Elymus adult

Elymus seedling

Microstegium

Microstegium litter
```

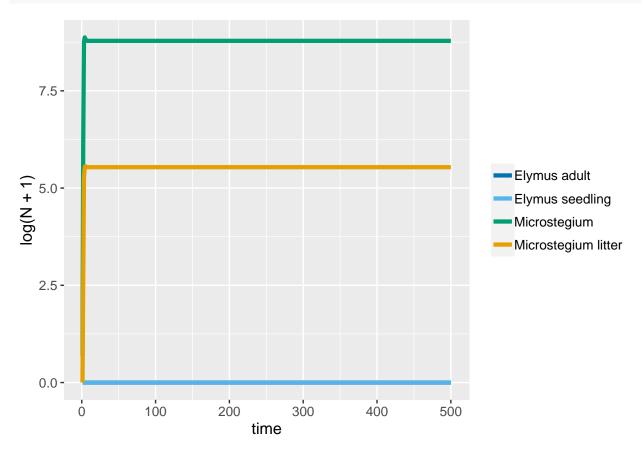
6.3 No disease, co-introduced



6.4 Disease, Microstegium by itself

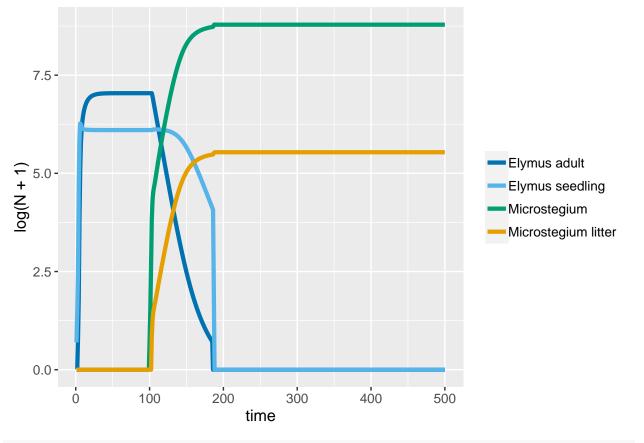
```
# run simulation
dis_mv_alone_sim <- simFun(params_dis, NO.A, NO.S = 0, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "none")
# figure of time series
dis_mv_alone_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    theme(axis.text = element_text(size = axisText),
        axis.title = element_text(size = axisTitle),
        legend.text = element_text(size = legendText),
```

```
legend.title = element_text(size = legendTitle)) +
scale_color_manual(values = colPal)
```

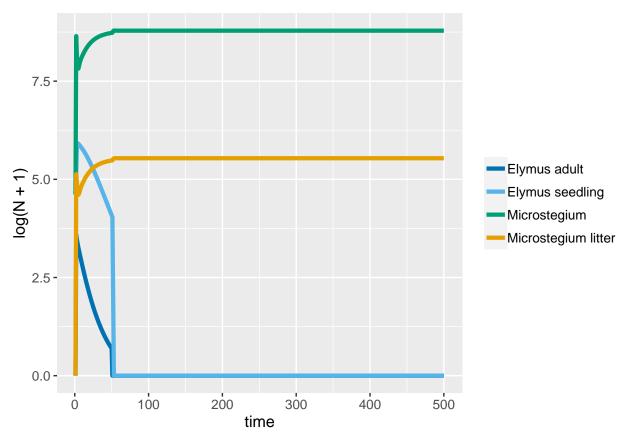


6.5 Disease, Microstegium invades Elymus

```
# run simulation
dis_mv_invades_sim <- simFun(params_dis, NO.A = 0, NO.S, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "annua
# figure of time series
dis_mv_invades_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    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)) +
    scale_color_manual(values = colPal)
```



6.6 Disease, co-introduced



6.7 No disease, Elymus by itself

```
legend.title = element_text(size = legendTitle)) +
scale_color_manual(values = colPal)
```

```
7.5 - Elymus adult Elymus seedling Microstegium Microstegium Microstegium litter
```

6.8 No disease, Elymus invades Microstegium

```
# run simulation
no_dis_ev_invades_sim <- simFun(params, NO.A, NO.S = 0, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "perenn
# figure of time series
no_dis_ev_invades_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    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)) +
scale_color_manual(values = colPal)
```

```
7.5 - Elymus adult Elymus seedling Microstegium Microstegium Microstegium litter
```

6.9 Disease, Elymus by itself

```
# run simulation
dis_ev_alone_sim <- simFun(params_dis, NO.A = 0, NO.S, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "none")
# figure of time series
dis_ev_alone_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    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)) +
scale_color_manual(values = colPal)
```

```
Elymus adult
Elymus seedling
Microstegium
Microstegium litter
```

6.10 Disease, Elymus invades Microstegium

```
# run simulation
dis_ev_invades_sim <- simFun(params_dis, NO.A, NO.S = 0, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "perent"
# figure of time series
dis_ev_invades_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    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)) +
scale_color_manual(values = colPal)
```

```
7.5-

Elymus adult

Elymus seedling

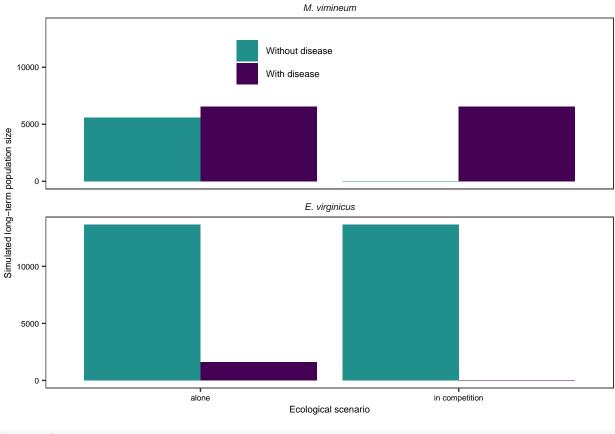
Microstegium

Microstegium litter
```

7 Population Figure

```
# combine data
pop_fig_dat <- no_dis_mv_alone_pop %>%
full_join(no_dis_co_intro_mv_pop) %>%
full_join(dis_mv_alone_pop) %>%
full_join(dis_co_intro_mv_pop) %>%
full_join(no_dis_ev_alone_pop) %>%
full_join(no_dis_co_intro_ev_pop) %>%
full_join(dis_ev_alone_pop) %>%
full_join(dis_ev_alone_pop) %>%
full_join(dis_co_intro_ev_pop) %>%
mutate(species = recode(species, "Microstegium" = "M. vimineum", "Elymus" = "E. virginicus") %>%
```

```
fct_relevel("M. vimineum"),
         log_N = log(N + 1),
         disease = fct_relevel(disease, "Without disease"))
## Joining, by = c("time", "N", "species", "disease", "interaction")
## Joining, by = c("time", "N", "species", "disease", "interaction")
## Joining, by = c("time", "N", "species", "disease", "interaction")
## Joining, by = c("time", "N", "species", "disease", "interaction")
## Joining, by = c("time", "N", "species", "disease", "interaction", "Elymus_seedling", "Elymus_adult")
## Joining, by = c("time", "N", "species", "disease", "interaction", "Elymus_seedling", "Elymus_adult")
## Joining, by = c("time", "N", "species", "disease", "interaction", "Elymus_seedling", "Elymus_adult")
# template theme
temp_theme <- theme_bw() +</pre>
  theme(axis.text = element_text(size = 6, color="black"),
        axis.title = element_text(size = 7),
        panel.background = element_blank(),
        panel.grid.major = element_blank(),
        panel.grid.minor = element_blank(),
        legend.text = element_text(size = 7),
        legend.title = element_blank(),
        legend.box.margin = margin(-10, -10, -10, -10),
        legend.position = c(0.42, 0.89),
        strip.background = element_blank(),
        strip.text = element_text(size = 7, face = "italic"),
        strip.placement = "outside",
        plot.title = element_text(size = 7, hjust = 0.5))
# colors
col pal = c("#21908CFF", "#440154FF")
# figure
pop_fig <- ggplot(pop_fig_dat, aes(x = interaction, y = N)) +</pre>
  geom_bar(stat = "identity", position = "dodge", aes(fill = disease)) +
  scale_fill_manual(values = col_pal) +
  facet_wrap(~species, nrow = 2) +
  xlab("Ecological scenario") +
  ylab("Simulated long-term population size") +
  temp_theme
pop_fig
```



```
# save figure
pdf("../output/simulated_long_term_pop_figure.pdf", width = 2, height = 4)
pop_fig
dev.off()
```

pdf ## 2