microstegium_elymus_model_summary

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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_072420.csv", col_types = cols())</pre>
params_dis <- read_csv(".../data/mv_ev_model_disease_parameters_experiment_072420.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 = 10000
# invasion time
invtime = 6000
```

```
# 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 intercept	y.Aint	34.1500	seeds g ⁻¹ year ⁻¹
annual biomass-seed conversion slope	y.A	0.8400	log-seeds log-g ⁻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	0.0270	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 intercept	y.Sint	3.8300	seeds g ⁻¹ year ⁻¹
perennial seedling biomass-seed conversion slope	y.S	0.8800	log-seeds log-g ⁻¹
perennial adult biomass-seed conversion intercept	y.Pint	6.5800	seeds g ⁻¹ year ⁻¹
perennial adult biomass-seed conversion slope	y.P	1.1900	log-seeds log-g ⁻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	V
litter suppression of annual germination	beta.A		$g^{-1} year^{-1}$
annual seed survival	s.A	0.1250	$year^{-1}$

parameter	symbol	value	units
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
interspecific adult effect of competition on annual	alpha.AP	0.1300	year ⁻¹
annual biomass-seed conversion intercept	y.Aint	34.1500	seeds g^{-1} year ⁻¹
annual biomass-seed conversion slope	y.A	0.8400	\log -seeds \log -g ⁻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	0.0270	$g^{-1} year^{-1}$
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 intercept	y.Sint	3.8300	seeds g ⁻¹ year ⁻¹
perennial seedling biomass-seed conversion slope	y.S	0.8800	log-seeds log-g ⁻¹
perennial adult biomass-seed conversion intercept	y.Pint	6.5800	seeds g ⁻¹ year ⁻¹
perennial adult biomass-seed conversion slope	y.P	1.1900	log-seeds log-g ⁻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{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{Y.S} * \text{N.S[t]} + \text{h.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

$$G.A = g.A / (1 + beta.A * L[t])$$
 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

4.3 Density-dependence on growth

```
V.A = v.A \ / \ (1 + alpha.AA * G.A * N.A[t] + alpha.AP * N.P[t] + alpha.AS * 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 * N.A[t] + alpha.SP * N.P[t] + alpha.SS * 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 * N.A[t] + alpha.PP * N.P[t] + alpha.PS * 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)
```

4.4 Seed production based on biomass

```
Y.A = V.A^y.A * y.Aint annual seed production = annual biomass with conversion factors (from a log-log regression)
```

```
Y.S = V.S^v.S * v.Sint - 1
```

perennial seedling seed production = perennial seedling biomass with conversion factors (from a log-log regression, 1 added to seed numbers before log-transforming)

```
Y.P = V.P^y.P * y.Pint - 1
```

perennial adult seed production = perennial adult biomass with conversion factors (from a log-log regression, 1 added to seed numbers before log-transforming)

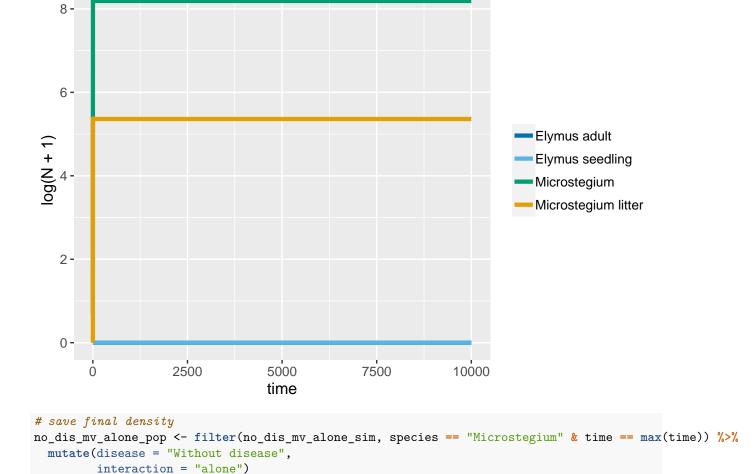
5 Function

```
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")$value
  y.Aint = filter(params, symbol == "y.Aint")$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
```

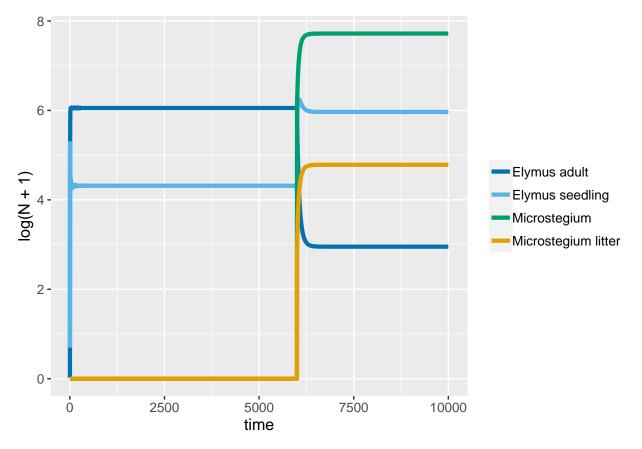
```
alpha.SA = filter(params, symbol == "alpha.SA")$value
alpha.SS = filter(params, symbol == "alpha.SS")$value
alpha.SP = filter(params, symbol == "alpha.SP")$value
alpha.PA = filter(params, symbol == "alpha.PA")$value
alpha.PS = filter(params, symbol == "alpha.PS")$value
alpha.PP = filter(params, symbol == "alpha.PP")$value
y.S = filter(params, symbol == "y.S")$value
y.Sint = filter(params, symbol == "y.Sint")$value
y.P = filter(params, symbol == "y.P")$value
y.Pint = filter(params, symbol == "y.Pint")$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 growth due to competition
 V.A = v.A / (1 + alpha.AA * G.A * N.A[t] + alpha.AP * N.P[t] + alpha.AS * G.S * N.S[t])
 V.S = v.S / (1 + alpha.SA * G.A * N.A[t] + alpha.SP * N.P[t] + alpha.SS * G.S * N.S[t])
 V.P = v.P / (1 + alpha.PA * G.A * N.A[t] + alpha.PP * N.P[t] + alpha.PS * G.S * N.S[t])
  # seed production based on biomass
 Y.A = V.A^y.A * y.Aint
  \# Y.S = V.S \hat{y}.S * y.Sint
 Y.S = V.S^y.S * y.Sint - 1
 Y.S = ifelse(Y.S < 0, 0, Y.S)
  \# Y.P = V.P \hat{y}.P * y.Pint
 Y.P = V.P^y.P * y.Pint - 1
 Y.P = ifelse(Y.P < 0, 0, Y.P)
  # population size
 N.A[t+1] = s.A * (1-G.A) * N.A[t] + G.A * h.A * Y.A * N.A[t]
```

6 Simulations

6.1 No disease, Microstegium by itself

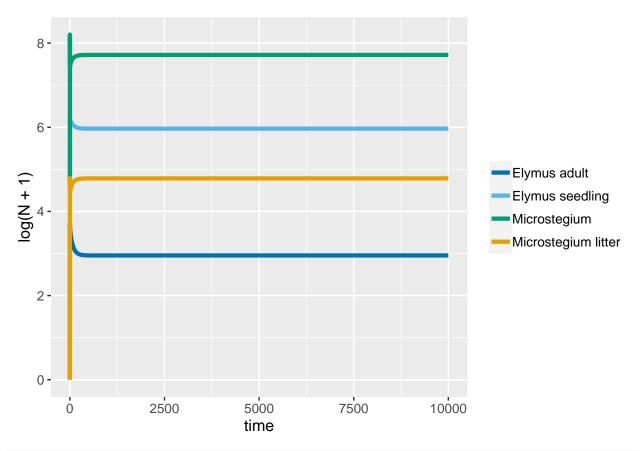


6.2 No disease, Microstegium invades Elymus



6.3 No disease, co-introduced

```
# run simulation
no_dis_co_intro_sim <- simFun(params, NO.A = 100, NO.S = 100, NO.P, LO, Ni.A, Ni.S, simtime, invtime,
# figure of time series
no_dis_co_intro_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)
```



6.4 Disease, Microstegium by itself

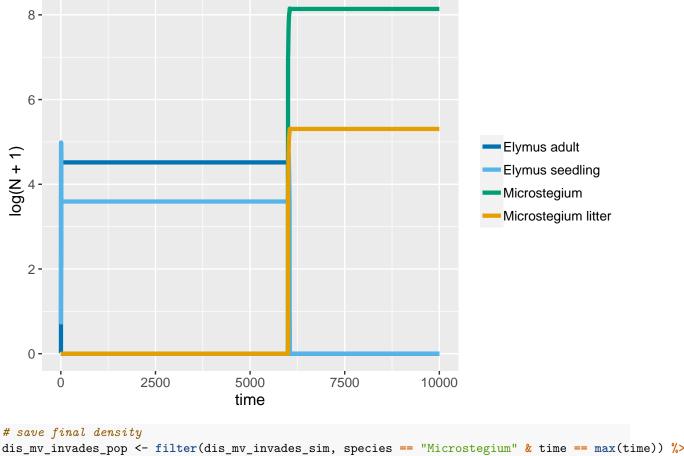
```
# run simulation
dis_mv_alone_sim <- simFun(params_dis, NO.A, NO.S = 0, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "none")
# figure of time series
dis_mv_alone_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    theme(axis.text = element_text(size = axisText),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

```
legend.title = element_text(size = legendTitle)) +
  scale_color_manual(values = colPal)
   8 -
   6 -
                                                                            Elymus adult
(1 + N)gol
                                                                             Elymus seedling
                                                                            Microstegium
                                                                             Microstegium litter
   2-
   0 -
                     2500
                                   5000
                                                  7500
                                                                10000
        Ö
                                   time
# save final density
dis_mv_alone_pop <- filter(dis_mv_alone_sim, species == "Microstegium" & time == max(time)) %>%
  mutate(disease = "With disease",
```

6.5 Disease, Microstegium invades Elymus

interaction = "alone")

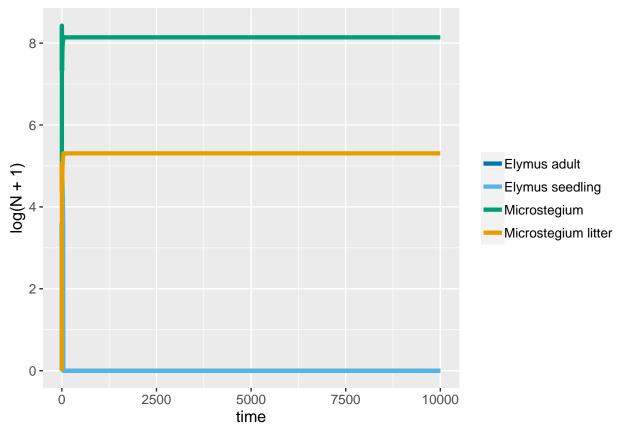
```
# run simulation
dis_mv_invades_sim <- simFun(params_dis, NO.A = 0, NO.S, NO.P, LO, Ni.A, Ni.S, simtime, invtime, "annua
# figure of time series
dis_mv_invades_sim %>%
    ggplot(aes(x = time, y = log(N+1), color = species)) +
    geom_line(size = 1.5) +
    theme(axis.text = element_text(size =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

```
# run simulation
dis_co_intro_sim <- simFun(params_dis, NO.A = 100, NO.S = 100, NO.P, LO, Ni.A, Ni.S, simtime, invtime,

# figure of time series
dis_co_intro_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)
```



6.7 No disease, Elymus by itself

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

```
Elymus adult
Elymus seedling
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)
```

```
Elymus adult
Elymus seedling
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),
```

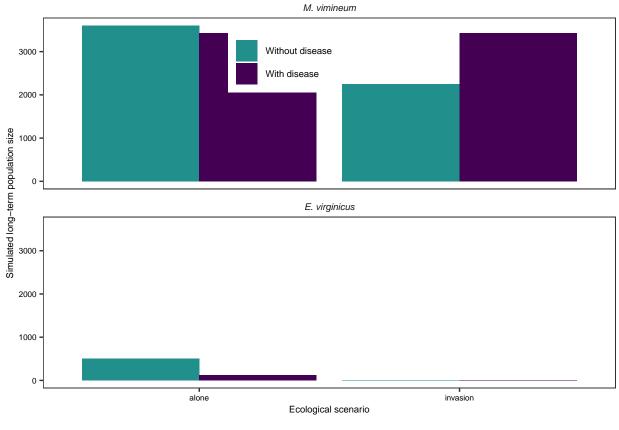
```
legend.title = element_text(size = legendTitle)) +
scale_color_manual(values = colPal)
```

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

7 Population Figure

```
# combine data
pop_fig_dat <- no_dis_mv_alone_pop %>%
full_join(no_dis_mv_invades_pop) %>%
full_join(dis_mv_alone_pop) %>%
full_join(dis_mv_invades_pop) %>%
full_join(no_dis_ev_alone_pop) %>%
full_join(no_dis_ev_invades_pop) %>%
full_join(dis_ev_alone_pop) %>%
full_join(dis_ev_alone_pop) %>%
full_join(dis_ev_invades_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