

Young Eastern White Pine and the White Pine Blister Rust Fungus

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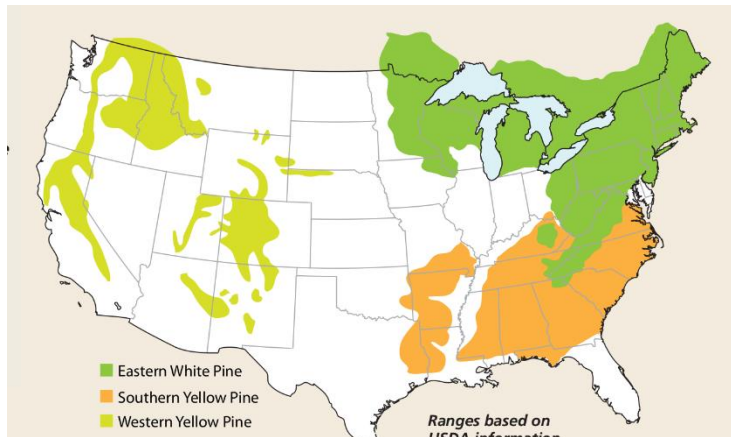
Introduction

Eastern White Pine

Eastern white pine (*Pinus strobus*) is one of the most valuable trees in North America, culturally, economically, and ecologically. This tree is the only five-needled white pine native to eastern North America, and it can be found all along the Appalachian Mountains and up into Ontario and Quebec.

Figure 1

Native Regions of White Pines



Note. From “Choosing Pine: Pine Grades,” by Ted Raife, 2019, Woodsmith, (<https://www.woodsmith.com/article/choosing-pine-pine-grades/>). Copyright 2023 by Active Interest Media company.

As one of the largest conifers in North America, these trees are typically seen 50 to 80 feet tall in landscapes but can grow upwards of 200 feet. The tree is also long-lived and can reach 200 years of age when undisturbed and can exceed 450 years as its maximum age (Wendel and Smith, 1990). White pine is commonly found in stands with other tree species (Fraedrich, n.d.) and is one of the most widely planted tree

species in eastern North America (Costanza et al., 2018).

The tree has many uses, including in the logging industry, the Christmas tree industry, reforestation projects, and is important for ecological biodiversity. During the 19th century, white pine became a popular tree for logging, as the consistency of its wood makes it great for furniture and woodcraft. The eastern white pine is also largely symmetrical, with horizontal and tiered branches, and has the unique ability to grow a crown of branches per year, making it a popular choice for a Christmas tree. The species is also highly versatile, as it can “grow from sea-level to 1220 m in elevation, on a wide variety of soils, and in 28 different forest cover-types” (Costanza et al., 2018). Despite having low shade tolerance when young, once established, *Pinus strobus* has a high growth rate compared to other trees, and with a strong root system, is a great tree of choice for reforestation, landscaping, and for windbreaks in forests. The eastern white pine is also culturally valuable to many groups in North America, including the Kitcisakik Algonquin community, the Menominee community, and the Iroquoian community.

Most importantly, these trees play a large role in their surrounding ecological communities. Depending on their location, white pine has the ability to function as a pioneer species, a physiographic climax species, or a long-lived successional species. The loss of these trees reduces the biodiversity of their habitat, as these tall trees provide food and shelter for many high dwelling animals, including bears, lynx, and many birds that

rely on the seeds the trees produce. In fact, whitebark pine trees have a mutualistic relationship with the Clark's Nutcracker and Gray Squirrels, who disperse the tree's seeds. Also, as with any sort of deforestation, the land of the area can become highly unstable. Without roots from trees and the presence of fauna and flora, the water retention of the land decreases, and areas become highly susceptible to erosion.

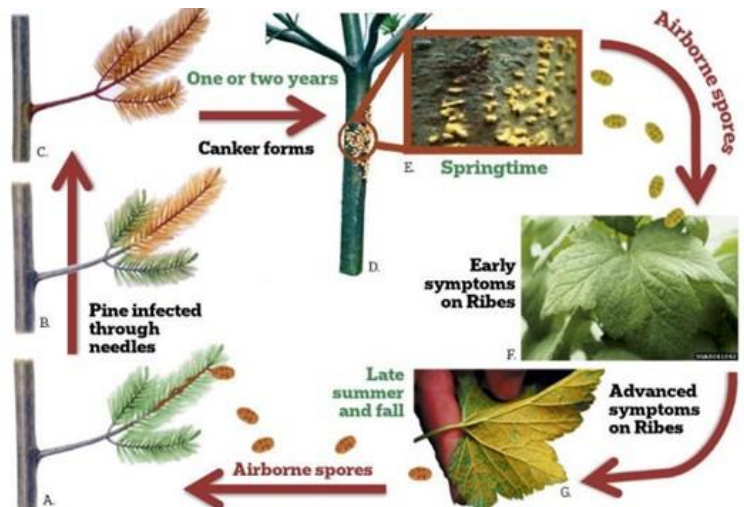
Like any other plant, eastern white pine trees can experience stress and will experience negative health effects. These trees are indicator trees of soil stress, and are especially sensitive to air pollution and salt. These trees enjoy moist, cool environments, and as climate change occurs over the next several decades, the regions suitable to eastern white pine will shift, and along with it, the population of eastern white pine.

White Pine Blister Rust

White pine blister rust (WPBR) is one of the many invasive forest diseases that poses a threat to North American forests. Known as *Cronartium ribicola*, WPBR is a fungus that affects five-needle (white) pines. Originally from eastern Asia, it was transported to Europe in the early 1700s and later to North America. Due to extensive logging during the late 1800s, eastern white pine seedlings that contained the fungus were imported from Europe, and the rust spread rapidly. While native to Asia, *C. ribicola* is invasive in North America and has killed off many of the western white pine and sugar pine in northwestern states, and currently poses most of a threat to high-elevation white pines. Currently, dead and dying whitebark pine trees can be seen in several parks, including Crater Lake National Park, Glacier National Park, and North Cascades National

Park (*White Pine Blister Rust and its Threat to High Elevation White Pines*, n.d.).

Figure 2
Simplified Life Cycle of White Pine Blister Rust



Note. From "White Pine Blister Rust", 2023, Invasive Species Centre, <https://www.invasivespeciescentre.ca/invasive-species/meet-the-species/invasive-pathogens/white-pine-blister-rust/>. Copyright 2023 by Invasive Species Centre.

White pine blister rust is a unique infection in that it requires two hosts: a white pine and *Ribes spp.* (a currant or a gooseberry plant). In late summer/early fall, cool and moist air currents carry spores from infected *Ribes spp.* The spores germinate on the surface of the needle and grow into the pine through any openings. Yellow or orange spots can be seen on the needle shortly after infection, and as the fungus continues to infect the pine, the infected branch swells. Over time, the fungus continues to grow into the infected needle, moving into a branch, where orange cankers will form. These cankers will eventually swell, and may secrete a heavy resin. The first summer after infection, the rust appears as orange blisters on cankers. At this point, the rust has the power to slowly stop nutrient flow further up the tree, causing topkill to occur. During the second spring after infection, white blisters appear on the

cankers, and when ready to crack, the blisters will turn yellow in color, and release aeciospores that infect the alternate host. These aeciospores travel through the air to infect the leaves of a *Ribes spp.* Two weeks after infection on the secondary host, urediniospores are created on the underside of *Ribes* leaves, which will release spores to infect other *Ribes* plants. During late summer/early fall, these spores will grow into hair-like projections, which produce basidiospores, which will be released to infect pines.

The white pine blister rust fungus moves through a branch toward the trunk of a tree, and will travel about 3 inches per year. For large and mature white pines, it can take multiple years for the fungus to kill the tree. During this time, topkill and the reduction of viable tree reduces cone and seed production, which can prevent the natural production of young trees. However, small and young trees can easily be killed within a few years of infection, as the rust has a smaller distance to travel to kill the trunk, and smaller trees have better conditions for infection to occur.

Climate and WPBR

Like most fungal pathogens, white pine blister rust favors moist, cool environments. Therefore, the cooler the summer, when basidiospores are released to infect white pines, the more favorable the conditions are for the spread of the rust. According to Arsdel (1972), “a tree in a moist site should always become infected more readily than its adjacent neighbors in drier sites.” He emphasizes the presence of dew on leaves in supercooled environments, and how the spacing of trees and the macroclimate influence the dewpoint temperature and the

presence of supercooled leaves that favor the formation of dew. Arsdel explains how the “bases of slopes, small narrow valleys, and small openings in the crown cover of the forest have abundant rust.” Bases of slopes create cold pools where WPBR will be prevalent, since drainage of nighttime air in these areas will create cool wet spots. In areas where there are small openings in the canopy, there is relatively little temperature change from the day and night due to the proximity of the trees. At night, plants growing in the opening are generally cooler than their surrounding air, often cooler than the dewpoint temperature. These cool spots have high relative humidities, and due to the little temperature change between night and day, also often have extended dew periods. The high humidity and supercooled leaves allow condensed water to form on leaves, which is an extremely favorable environment for rust. According to a study by White et al. (2002, as cited in Costanza et al., 2018) “cooler and moister sites in Minnesota had higher incidence of blister rust compared to pines grown at lower elevations with warmer and drier conditions.” The spread of WPBR should be monitored over the next decades, as the infection of white pines may grow significantly depending on how climates change in North America.

Young White Pine Trees

Young eastern white pine trees are most at risk if an epidemic of white pine blister rust were to occur. Since they are lower to the ground, they are closer to the cool, moist sites that WPBR seems to thrive in. Also, due to their small stature, once infected, it only takes a few years for the rust to reach their trunk and kill the young trees.

If an epidemic of white pine blister rust were to occur, mature trees would experience topkill and reduced regeneration due to the decrease in viable cone production. Along with the lack of cones to reproduce, young trees would die, effectively creating a large gap in generations or killing off a large portion of eastern white pine trees in forests in North America. The objective of this paper is to model how young eastern white pine trees interact with white pine blister rust with varying degrees of infection.

First, the term “young tree” should be defined. It takes about 3 to 5 years for an eastern white pine tree to become established due its slow initial growth compared to other tree species. After about 10 years, growth becomes quite rapid and seed production begins. Although eastern white pine trees continue reproducing until very late age, their seed production peaks at around 20-30 years of age. So, based on the rate of growth of young trees and their ability to reproduce, a “young” tree is going to be defined as a tree that is less than 30 years of age, which is comparatively young considering these trees can live upwards of 400 years.

Learning Goals

The aim of this project is to put together the skills I have learned over the semester to build a model that is either relevant towards my topic and answers the questions or gives me insight to the questions I have asked. Through this project, I want to learn how to implement the known life cycle of the white pine blister rust fungus, and model it to see how various variables that go into the effectiveness of the rust affect changes in the eastern white pine population.

I anticipate that any variables that account for increased stress of trees, climate change that leads to cooler and wetter summers, and climate change that leads to the increased presence of air pollutants over the regions of white pine, will be shown to increase rust effectiveness and therefore the number of infected trees.

Method

For this project, an SIRM age-structured model was used, as it could model very young trees (< 5 years) that were highly susceptible, and older trees (20 years) that were still susceptible but were experiencing much faster growth rates that would be impacted differently by the rust. The SIRM model also accounted for the random susceptibility found in forests due to genetic variation, the infection of trees to the rust, recovery, where a tree was pruned or the fungus was killed in an unviable environment, and mortality.

It should be noted that some assumptions that I am making in my model are that at least some or all trees are naturally susceptible to white pine blister rust, and that there are *Ribes spp.* nearby to enable the rust to go through its life cycle.

For this particular model, there were four age groups that were used: trees between 0 and 5 years of age, trees between 5 and 10 years of age, trees between 10 and 20 years of age, and trees between 20 to 30 years of age. The first two are “bins” of 5 years, since the first 5 years are during the establishment period and are when young trees are the most susceptible to the fungus. The next five years are important for establishment and growth into their reproductive age. At the age of 10, most trees have begun producing cones, and tree

growth is starting to increase. By the age of 20, most trees are reaching their most viable production of cones, and are outgrowing other species rapidly. The ODEs created for this model are as follows:

Seedlings (s): 0 to 5 years of age

$$\frac{dS_s}{dt} = -S_s\beta_s(\sigma)[I_s + I_p + I_e + I_y] - \alpha S_s$$

$$\frac{dI_s}{dt} = -I_s(\gamma_s + \alpha) + \beta_s(\sigma)[I_s + I_p + I_e + I_y](S_s + R_s)$$

$$\frac{dR_s}{dt} = -\beta_s(\sigma)[I_s + I_p + I_e + I_y]R_s + p_s(\sigma)\gamma_s - \alpha R_s$$

$$\frac{dM_s}{dt} = (1 - p_s(\sigma))\gamma_s I_s$$

Saplings (p): 5 to 10 years of age

$$\frac{dS_p}{dt} = \alpha S_s - S_p\beta_p(\sigma)[I_s + I_p + I_e + I_y] - \alpha S_p$$

$$\frac{dI_p}{dt} = -I_p(\gamma_p + \alpha) + \beta_p(\sigma)[I_s + I_p + I_e + I_y](S_p + R_p) + I_s\alpha$$

$$\frac{dR_p}{dt} = \alpha R_s - R_p\beta_p(\sigma)[I_s + I_p + I_e + I_y] + p_p(\sigma)\gamma_p - \alpha R_p$$

$$\frac{dM_p}{dt} = (1 - p_p(\sigma))\gamma_p I_p$$

Established (e): 10 to 20 years of age

$$\frac{dS_e}{dt} = \alpha S_p - S_e\beta_e(\sigma)[I_s + I_p + I_e + I_y] - \omega S_e$$

$$\frac{dI_e}{dt} = -I_e(\gamma_e + \omega) + \beta_e(\sigma)[I_s + I_p + I_e + I_y](S_e + R_e) + I_p\alpha$$

$$\frac{dR_e}{dt} = \alpha R_p - R_e\beta_e(\sigma)[I_s + I_p + I_e + I_y] + p_e(\sigma)\gamma_e - \omega R_e$$

$$\frac{dM_e}{dt} = (1 - p_e(\sigma))\gamma_e I_e$$

Young tree (y): 20 to 30 years of age

$$\frac{dS_y}{dt} = \omega S_e - S_y\beta_y(\sigma)[I_s + I_p + I_e + I_y]$$

$$\frac{dI_y}{dt} = -I_y(\gamma_y) + I_e\omega + \beta_y(\sigma)[I_s + I_p + I_e + I_y](S_y + R_y)$$

$$\frac{dR_y}{dt} = \omega R_e - R_y\beta_y(\sigma)[I_s + I_p + I_e + I_y] + p_y(\sigma)\gamma_y$$

$$\frac{dM_y}{dt} = (1 - p_y(\sigma))\gamma_y I_y$$

Full explanations of each variable/character can be seen in Appendix 1 and a visual diagram of this model can be seen in Appendix 2. Based on reports of various age structures of trees in forests, it was decided that 17% of the population would consist of trees 0 – 5 years old, 11% of the population would consist of young trees 5 – 10 years old, 29% of the population would consist of trees 10 – 20 years old, and 43% of the population would consist of trees that are 20 – 30 years old, where 100% of the population are trees less than 30 years of age. One of the most important parts of the model are the $\beta_x(\sigma)$ and $p_x(\sigma)$ equations, which model the different mortality rates trees can experience as they grow. Since younger trees are more susceptible to the fungus, and can reach up to 90% mortality in some cases (Costanza et al.), the equations for $\beta_s(\sigma)$, $\beta_p(\sigma)$, $p_s(\sigma)$ and $p_p(\sigma)$ reflect that. The equations chosen can be found in Appendix 1.

The only conditions that were changed for this model were the initial conditions for the infected population. According to Lombard and Bofinger (1999), infected ranges due to WPBR can range from 0 to around 7.3%. The five conditions tested can be seen in Table 1:

Table 1

Initial conditions for infected individuals:

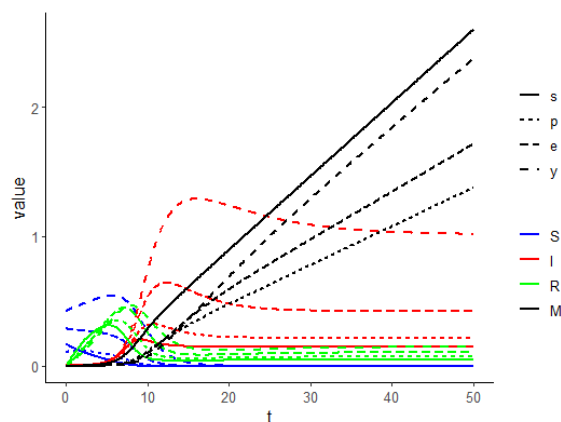
| % of infected individuals | 0.01 | 0.025 | 0.035 | 0.05 | 0.07 |
|---------------------------|--------|---------|---------|--------|--------|
| 's' infected individuals | 0.0017 | 0.00425 | 0.00595 | 0.0085 | 0.0119 |
| 'p' infected individuals | 0.0011 | 0.00275 | 0.00385 | 0.0055 | 0.0077 |
| 'e' infected individuals | 0.0029 | 0.00725 | 0.01015 | 0.0145 | 0.0203 |
| 'y' infected individuals | 0.0043 | 0.01075 | 0.01515 | 0.0215 | 0.0301 |

Each of these infected values were tested for low, medium, and high susceptibility conditions, which relied on tree stress and climate. The values of σ tested were 0.3, 0.6, and 0.9. The production of all 15 tables can be found in Appendix 3.

Findings and Results

Figure 3

Model for 1% of population infected ($\sigma = 0.3$)

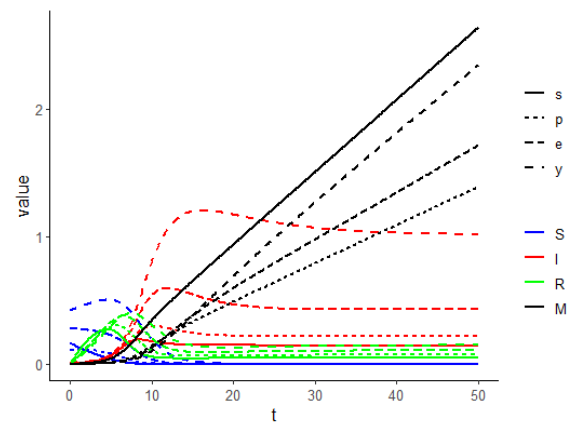


This model shows that there is an initial decrease in susceptible trees, and a slight

increase which can be accounted for by trees aging and moving into an upper age group. This model also shows that there is a high proportion of trees that are ages 10 to 20 and 20 to 30 that are infected. Mortality is also the worst for the youngest trees, but trees 20 to 30 years of age are also experiencing high levels of mortality.

Figure 4

Model for 2.5% of the population infected ($\sigma = 0.3$)



This model is similar to the first one, and shows that the youngest trees are experiencing the highest rates of mortality, but there is less of a spike in infected, and the proportion of infected seems to largely stay the same. This makes sense, because eastern white pines cannot recover fully or gain resistance from the fungus. Instead, the fungus must experience conditions it cannot survive in, the branches on the tree must be pruned, or the tree experiences mortality. These trends continue for the next few graphs; trees ages 0 to 5 are experiencing the highest rates of mortality, and the infected curves are becoming more and more level with their highest point.

For all populations, regardless of the proportion of initial infected, with a sigma value of 0.3, all models show that the

highest mortality rates occur in the youngest trees 0 to 5 years of age; at sigma values of 0.6 and 0.9, trees of ages 20 to 30 appear to have the highest mortality rates. Besides this, all models appear to follow the same trend.

Discussion and Conclusions

Even at the lowest proportions of infected trees in the population, mortality among trees seems to quickly occur and the remaining individuals in the population are infected and will likely die in the future. This goes to show that young eastern white pine trees are under serious threat to white pine blister rust, even under relatively low proportions of infected among young trees. As stress of trees increases and conditions for white pine blister rust are favored, the rate at which mortality occurs increases. As the proportion of individuals initially infected in the population increases, there is less of a “spike” in initially infected individuals, as instead the lines level off quickly, telling us that a large proportion of young trees are susceptible and in the coming years, as conditions for white pine blister rust improve and stress factors on eastern white pine trees increase, an epidemic among young individuals is likely to occur.

Outlook and Future Work

As our climate changes, it is important to note that optimal areas for various organisms will change, and many will struggle to adapt to the change that is occurring so fast. However, this may benefit some organisms, such as the invasive white pine blister rust, and outbreaks and epidemics may occur, placing even more stress on the increasingly stressed environment.

The next thing to look at would be modelling an epidemic among young trees against a forest of all ages of eastern white pine, and observing how white pine blister rust impacts various ages of eastern white pine.

It would also be interesting to model the rust spatially, according to how close or far trees are from each other, where they are located geographically (like a base of a hill), and where secondary hosts are located. This second model would be much more complicated, as it involves real data, or at least simulated data that would be extrapolated from a region. These models would provide much insight into how various areas could be impacted by white pine blister rust, effectively reducing the chance of an epidemic, and modelling various climate models on top of these spatial models to predict epidemics in forests that respond in different ways to changes in our climate.

I would have been interested in spending more time adjusting the various functions and constants that were chosen, and coming up with some values that can accurately represent various variables seen in ecosystems. For example, I would like to have explored better equations for stress or disease effectiveness that takes into account other variables, rather than me assigning a constant to it.

Overall, these models barely touch the surface when it comes to climate change and its impact on forest fungi. Better data on forests, and models for climate change, should be implemented together to more accurately see how our forests are changing and how we can plan for the future to

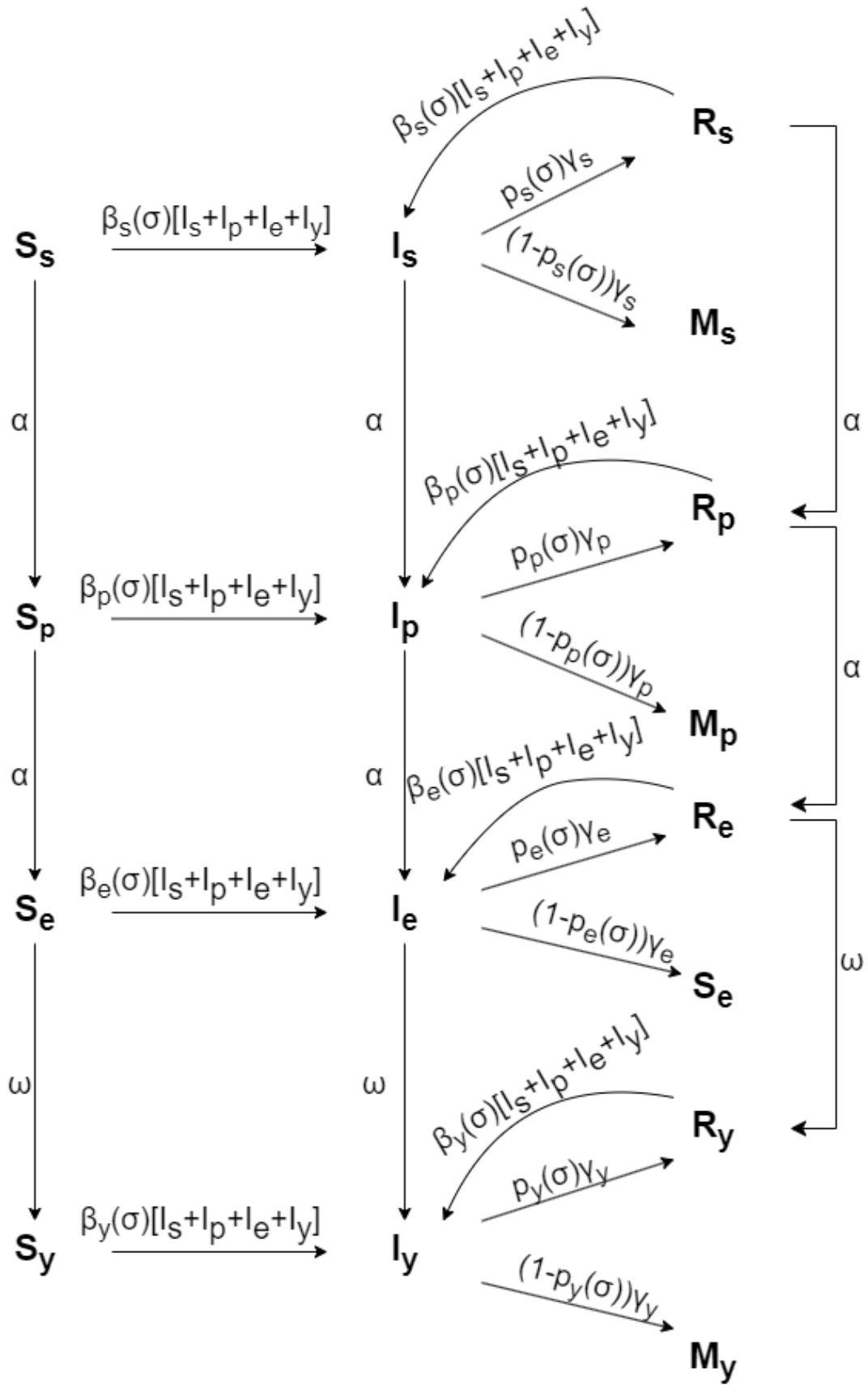
promote the longevity of all flora and fauna
in the environment.

Appendix 1

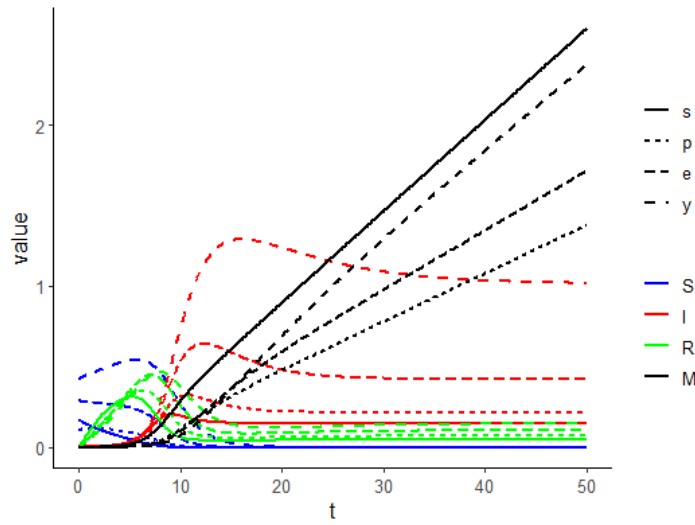
- S_s : the proportion of susceptible trees 0 to 5 years of age
- S_p : the proportion of susceptible trees 5 to 10 years of age
- S_e : the proportion of susceptible trees 10 to 20 years of age
- S_y : the proportion of susceptible trees 20 to 30 years of age
- I_s : the proportion of infected trees 0 to 5 years of age
- I_p : the proportion of infected trees 5 to 10 years of age
- I_e : the proportion of infected trees 10 to 20 years of age
- I_y : the proportion of infected trees 20 to 30 years of age
- R_s : the proportion of recovered trees 0 to 5 years of age
- R_p : the proportion of recovered trees 5 to 10 years of age
- R_e : the proportion of recovered trees 10 to 20 years of age
- R_y : the proportion of recovered trees 20 to 30 years of age
- M_s : the proportion of dead trees 0 to 5 years of age
- M_p : the proportion of dead trees 5 to 10 years of age
- M_e : the proportion of dead trees 10 to 20 years of age
- M_y : the proportion of dead trees 20 to 30 years of age
- $\beta_s(\sigma)$: a function of tree susceptibility for trees 0 to 5 years of age
 - o $\beta_s(\sigma) = 1/2 + 2\sigma$
- $\beta_p(\sigma)$: a function of tree susceptibility for trees 5 to 10 years of age
 - o $\beta_p(\sigma) = (1/5) + (\frac{4}{5})\sigma$
- $\beta_e(\sigma)$: a function of tree susceptibility for trees 10 to 20 years of age
 - o $\beta_e(\sigma) = (1/7) + (\frac{4}{7})\sigma$
- $\beta_y(\sigma)$: a function of tree susceptibility for trees 20 to 30 years of age
 - o $\beta_y(\sigma) = (1/10) + (\frac{2}{5})\sigma$
- α : the time it takes for a tree to move from 's' to 'p' or 'p' to 'e'
 - o $\alpha = 1/5 \text{ years}^{-1}$
- ω : the time it takes for a tree to move from 'e' to 'y'
 - o $\omega = 1/10 \text{ years}^{-1}$
- γ_s : the rate at which 's' trees die to WPBR
 - o $\gamma_s = \frac{1}{2} \text{ years}^{-1}$
- γ_p : the rate at which 'p' trees die to WPBR
 - o $\gamma_p = \frac{1}{5} \text{ years}^{-1}$
- γ_e : the rate at which 'e' trees die to WPBR
 - o $\gamma_e = \frac{1}{7} \text{ years}^{-1}$
- γ_y : the rate at which 'y' trees die to WPBR
 - o $\gamma_y = \frac{1}{10} \text{ years}^{-1}$
- $p_s(\sigma)$: a function of proportion of 's' trees to recover
 - o $p_s(\sigma) = 0.30 - 0.25\sigma$

- $p_p(\sigma)$: a function of proportion of 'p' trees to recover
 - o $p_s(\sigma) = 0.40 - 0.30\sigma$
- $p_e(\sigma)$: a function of proportion of 'e' trees to recover
 - o $p_s(\sigma) = 0.50 - 0.35\sigma$
- $p_y(\sigma)$: a function of proportion of 'y' trees to recover
 - o $p_y(\sigma) = 0.60 - 0.40\sigma$

Appendix 2

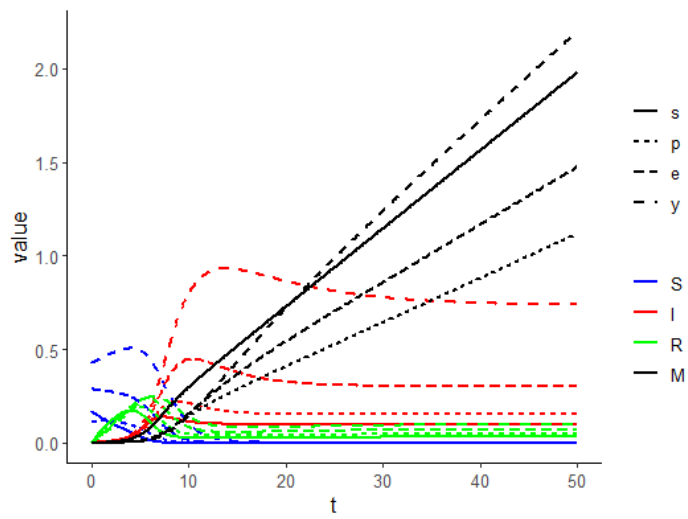


Appendix 3



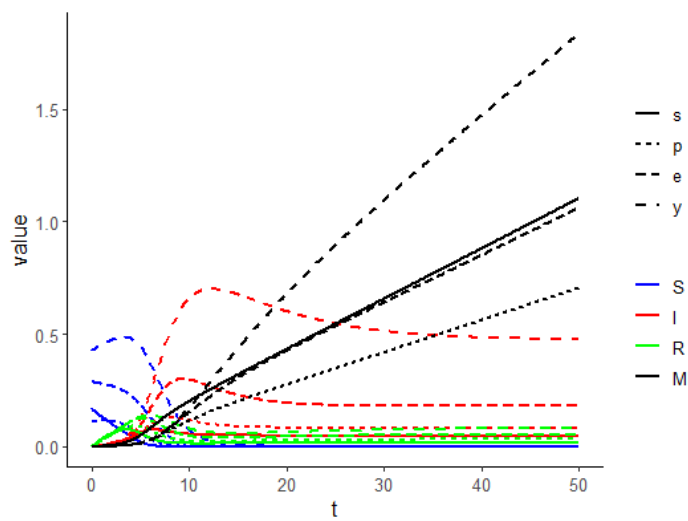
Proportion of infected: 0.01

$\sigma = 0.3$



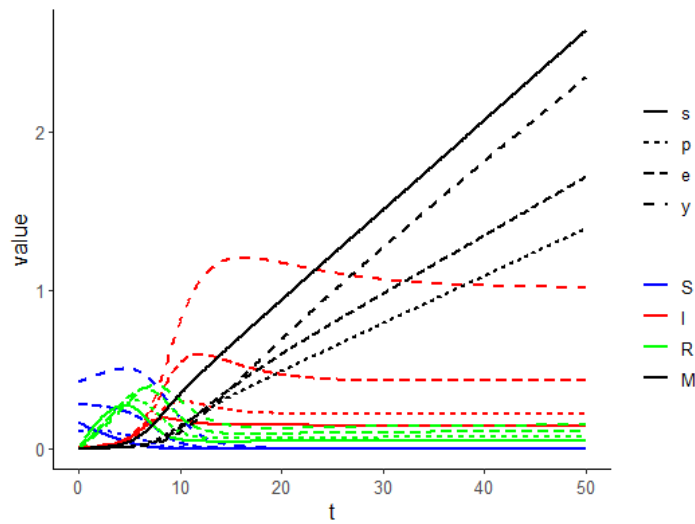
Proportion of infected: 0.01

$\sigma = 0.6$



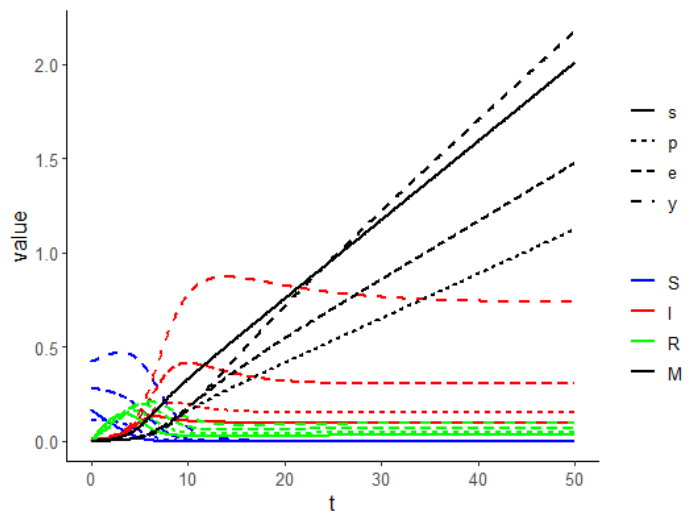
Proportion of infected: 0.01

$\sigma = 0.9$



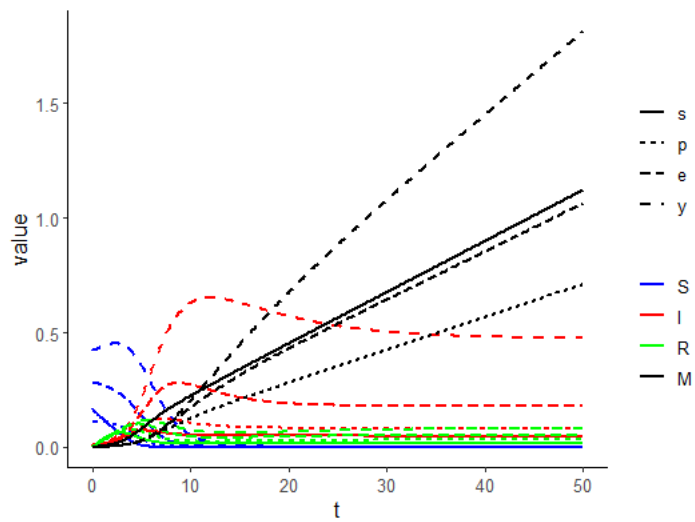
Proportion of infected: 0.025

$\sigma = 0.3$



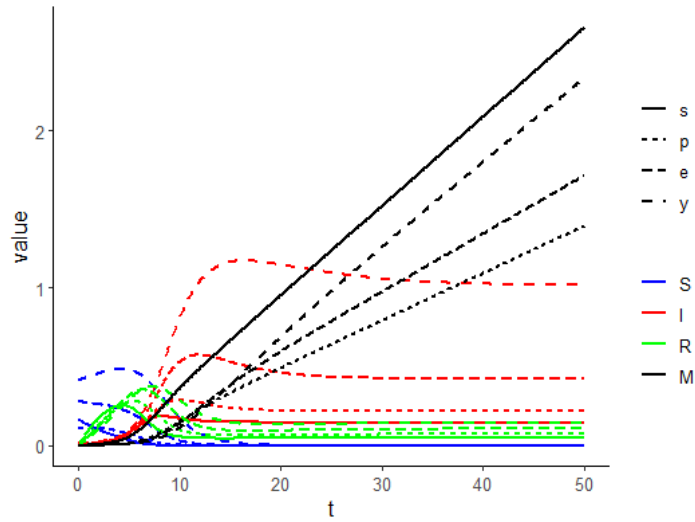
Proportion of infected: 0.025

$\sigma = 0.6$



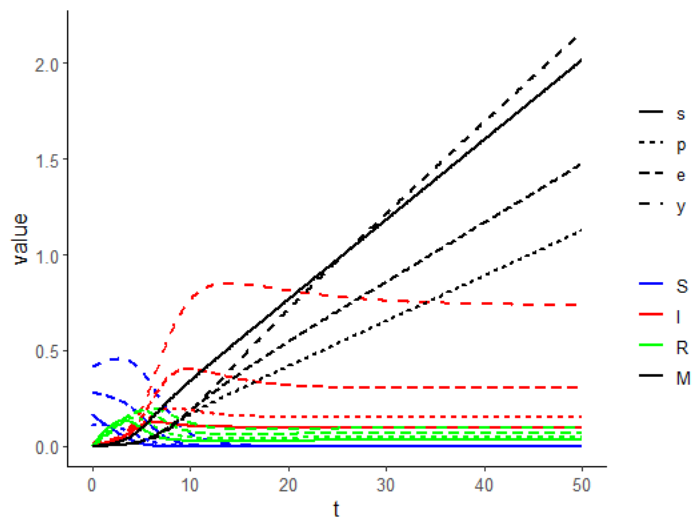
Proportion of infected: 0.025

$\sigma = 0.9$



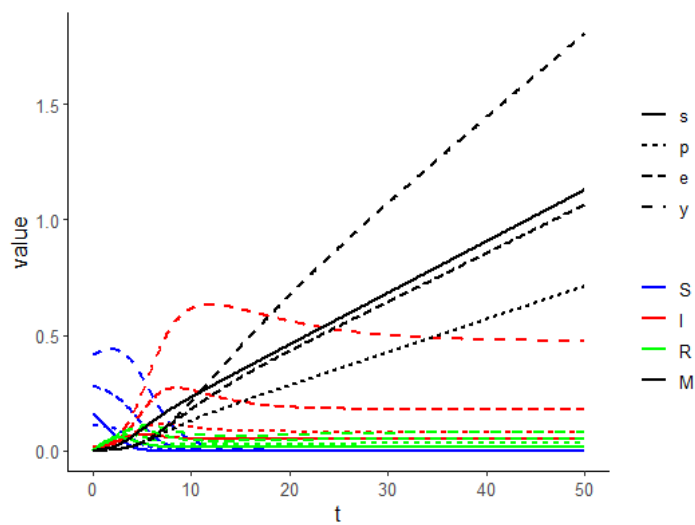
Proportion of infected: 0.035

$\sigma = 0.3$



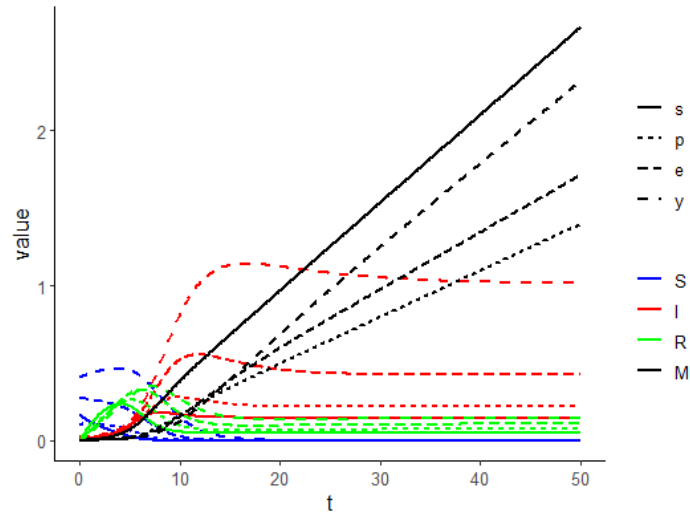
Proportion of infected: 0.035

$\sigma = 0.6$



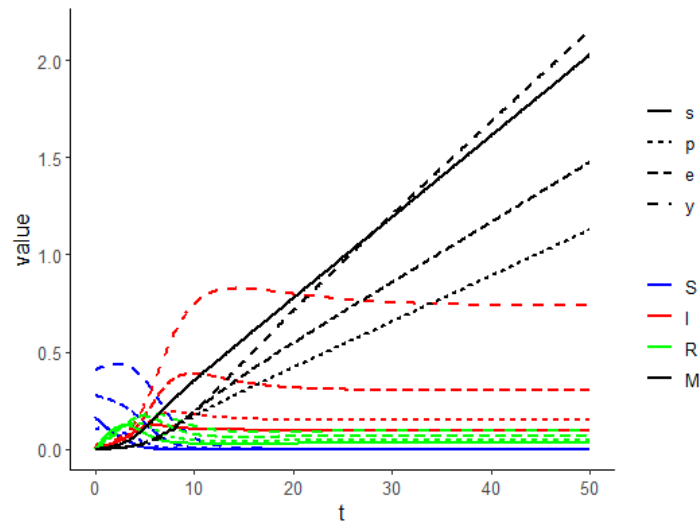
Proportion of infected: 0.035

$\sigma = 0.9$



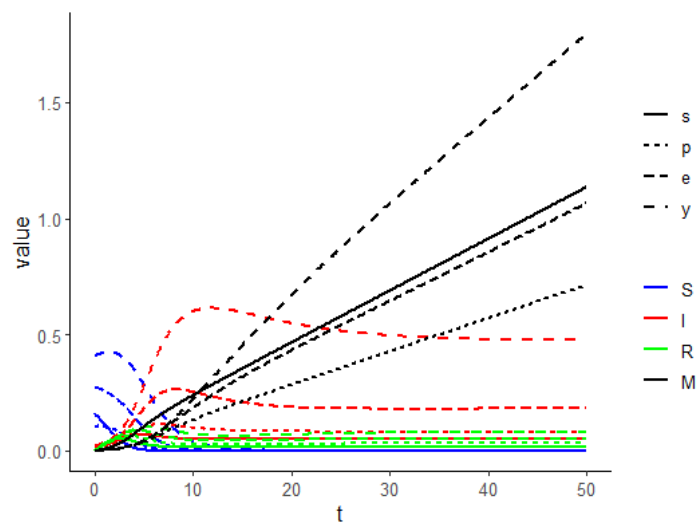
Proportion of infected: 0.05

$\sigma = 0.3$



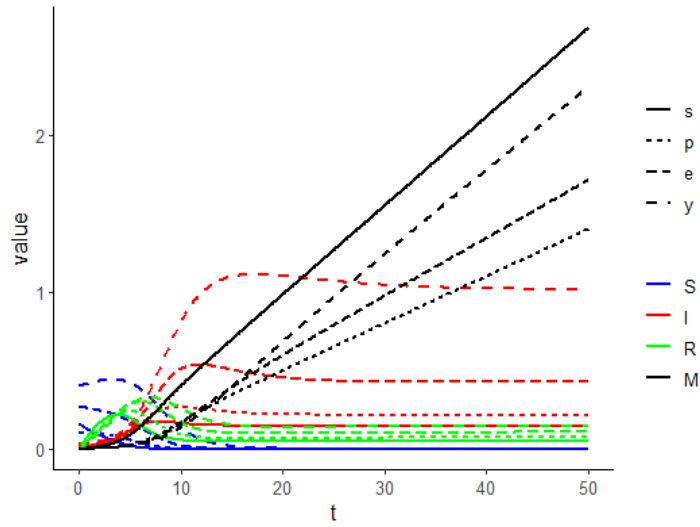
Proportion of infected: 0.05

$\sigma = 0.6$



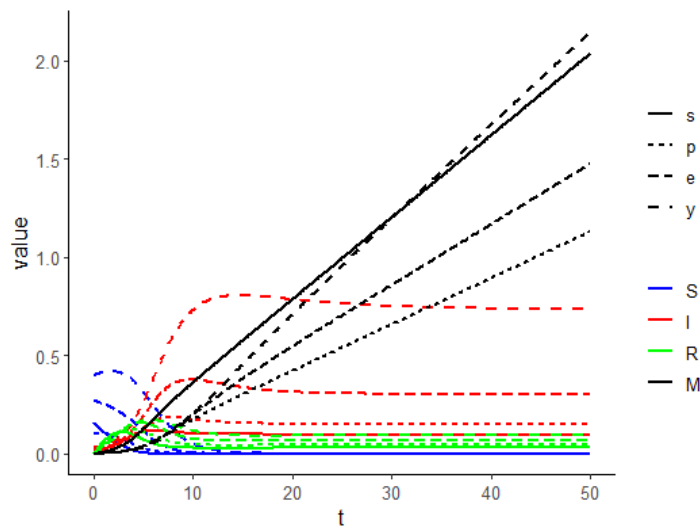
Proportion of infected: 0.05

$\sigma = 0.9$



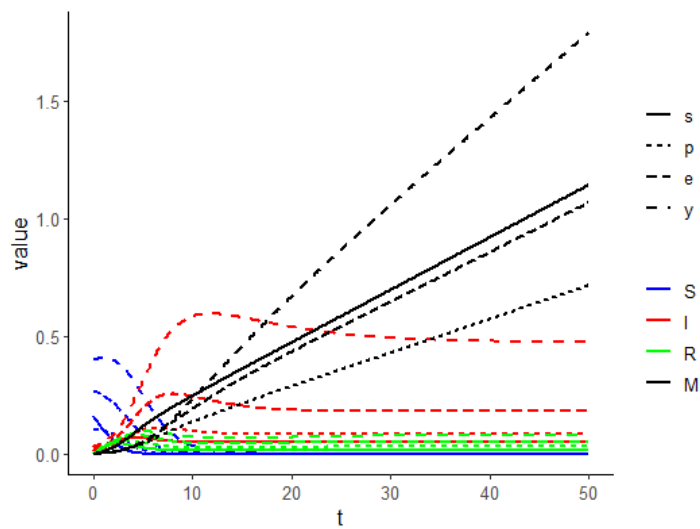
Proportion of infected: 0.07

$\sigma = 0.3$



Proportion of infected: 0.07

$\sigma = 0.6$



Proportion of infected: 0.07

$\sigma = 0.9$

Appendix 4

```

1 library(tidyverse)
2 library(odin)
3
4 #SIRM Model for 4 Age Groups
5 #0-5yrs: Seedling (s)
6 #5-10yrs: sapling (p)
7 #10-20yrs: Established (e)
8 #20-30yrs: Young tree (y)
9
10 #Age Groups Model
11 sirm_age <- odin::odin({
12
13   deriv(Ss) <- -Ss*beta_s*(Is+Ip+Ie+Iy) - alpha*Ss
14   deriv(Is) <- -Is*(gamma_s + alpha) + beta_s*(Is+Ip+Ie+Iy)*(Ss + Rs)
15   deriv(Rs) <- -Rs*beta_s*(Is+Ip+Ie+Iy) + p_s*gamma_s - alpha*Rs
16   deriv(Ms) <- (1 - p_s)*gamma_s*Is
17
18   deriv(Sp) <- alpha*Ss - Sp*beta_p*(Is+Ip+Ie+Iy) - alpha*Sp
19   deriv(Ip) <- -Ip*(gamma_p + alpha) + beta_p*(Is+Ip+Ie+Iy)*(Sp + Rp) + alpha*Is
20   deriv(Rp) <- alpha*Rs - Rp*beta_p*(Is+Ip+Ie+Iy) + p_p*gamma_p - alpha*Rp
21   deriv(Mp) <- (1 - p_p)*gamma_p*Ip
22
23   deriv(Se) <- alpha*Sp - Se*beta_e*(Is+Ip+Ie+Iy) - omega*Se
24   deriv(Ie) <- -Ie*(gamma_e + omega) + beta_e*(Is+Ip+Ie+Iy)*(Se + Re) + alpha*Ip
25   deriv(Re) <- alpha*Rp - Re*beta_e*(Is+Ip+Ie+Iy) + p_e*gamma_e - omega*Re
26   deriv(Me) <- (1 - p_e)*gamma_e*Ie
27
28   deriv(Sy) <- omega*Se - Sy*beta_y*(Is+Ip+Ie+Iy)
29   deriv(Iy) <- -Iy*gamma_y + Ie*omega + beta_y*(Is+Ip+Ie+Iy)*(Sy + Ry)
30   deriv(Ry) <- omega*Re - Ry*beta_y*(Is+Ip+Ie+Iy) + p_y*gamma_y
31   deriv(My) <- (1 - p_y)*gamma_y*Iy
32
33   #Initial Conditions and Equations
34   #Infected has been found to vary between 0 and 7.3%
35   initial(Ss) <- (0.17)*(0.99)
36   initial(Is) <- (0.17)*(0.01)
37   initial(Rs) <- 0
38   initial(Ms) <- 0
39
40   initial(Sp) <- (0.11)*(0.99)
41   initial(Ip) <- (0.11)*(0.01)
42   initial(Rp) <- 0
43   initial(Mp) <- 0

```

```

44
45 initial(Se) <- (0.29)*(0.99)
46 initial(Ie) <- (0.29)*(0.01)
47 initial(Re) <- 0
48 initial(Me) <- 0
49
50 initial(Sy) <- (0.43)*(0.99)
51 initial(Iy) <- (0.43)*(0.01)
52 initial(Ry) <- 0
53 initial(My) <- 0
54
55 gamma_s <- user(0.5) #1/2 years^-1
56 gamma_p <- user(0.2) #1/5 years^-1
57 gamma_e <- user((1/7)) #1/7 years^-1
58 gamma_y <- user(0.1) #1/10 years^-1
59
60 #stress - pH, geography, elevation, climate change/pollution, shade/sunlight/growing conditions
61 #stress <- 0.5 #stress is a level between 0(not stressed at all) and 1(practically dead with stress)
62 #susceptibility <- 0.67 #susceptibility is a factor of age/height - the younger and shorter, the more susceptible
63 #effectiveness depends on the presence of secondary hosts, climate(the presence of supercooled leaves), and geography
64 #effectiveness <- 0.9 #a level between 0(rust is not present) and 1(incredibly effective)
65 # starting level of sigma is 0.27
66 #sigma <- stress*susceptibility*effectiveness #sigma is a value between 0 and 1
67 sigma <- 0.3
68
69 alpha <- 0.2 #1/5 years^-1
70 omega <- 0.1 #1/10 years^-1
71 beta_s <- 0.5 + 2*sigma
72 beta_p <- 0.2 + 0.8*sigma
73 beta_e <- (1/7) + (4/7)*sigma
74 beta_y <- 0.1 + 0.4*sigma
75 p_s <- 0.30 - 0.25*sigma
76 p_p <- 0.40 - 0.30*sigma
77 p_e <- 0.50 - 0.35*sigma
78 p_y <- 0.60 - 0.40*sigma
79 } })
80
81 model_age <- sirm_age$new()
82
83 t <- seq(from=0, to=50, by=0.1)
84 sol_age <- as_tibble(data.frame(model_age$run(t)))
85
86 sol_age %>%
87   pivot_longer(-t) %>%
88   mutate(compartment=substr(name,1,1)) %>%
89   mutate(agegrp=substr(name,2,2)) %>%
90   ggplot(aes(x=t, y=value, col=factor(compartment,levels=c("S","I","R","M")), lty=factor(agegrp,levels=c("s","p","e","y")))) +
91   geom_line(linewidth=1) +
92   scale_color_manual(values=c("S"="blue", "I"="red", "R"="green", "M"="black")) +
93   theme_classic() +
94   theme(text=element_text(size=12), legend.title=element_blank()) |

```

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