Basic model of infection biology

Based on Chap 11 – Evolution of Virulence
from "Evolutionary Dynamics"
by Martin A Nowak

Notation

X – density of uninfected individuals
Y – density of infected individuals

a – rate of addition of new uninfected individuals
v – death rate of uninfected individuals
$v + w$ – death rate of infected individuals
w is the virulence – *i.e.* the strenth of effect of the disease on the host
k – rate of spread of infection

$$\frac{dX}{dt} = a - vX - kXY$$

$$\frac{dY}{dt} = kXY - (v + w)Y$$

This is similar to the beetles program, but not the same.

What are the similarities and differences?

Death Terms: $-vX$ and $-(v+w)Y$

These are the same in the beetles model

Infection Term: kXY

In the beetles model the infection rate is also proportional to XY – a green tree is infected by a red tree. However, the beetles model has a spatial structure. The infection only spreads to a neighbouring tree. This important property is not included in the differential equation.

Tree Growth Term: a

This is quite different.

In the basic model, the rate of addition of trees is constant. This is not very realistic, but it makes the mathematical analysis easy. (Maybe the birds bring in seeds from outside the area being studied!)

In the beetles model, trees give birth to new trees in vacant neighbouring sites. This is approximately $rX(1-X/X_{max})$, but is more complicated than this because of the spatial correlations.

Implementation of Model in Netlogo (basicinfection1.nlogo)

```
to go
  set avnew a * atot * dt
  set nnew random-poisson avnew
  create-turtles nnew [
    set xcor random-xcor
    set ycor random-ycor
    set color green
    set shape "circle"
  ]

  set pinf k * y * dt

  ask turtles [
    if color = green [
      set rr random-float 1.0
      if rr < pinf [set color red]
      if rr >= pinf and rr < pinf + v * dt [die]
    ]
    if color = red [
      if random-float 1.0 < (v + w) * dt [die]
    ]
  ]
```

We can solve the steady state densities in this model exactly

1. If there is no infection: $\dfrac{dX}{dt} = a - vX$

Therefore, the steady state density of trees without infecton is $X = a/v$

2. If there is an infection: $\dfrac{dY}{dt} = Y(kX - (v + w))$

Therefore, dY/dt = 0 if
      (i) Y = 0
      (ii) Y ≠ 0, and $X = (v+w)/k$

3. In case (ii) we need to calculate Y.
We know that: $\dfrac{dX}{dt} = a - vX - kXY$
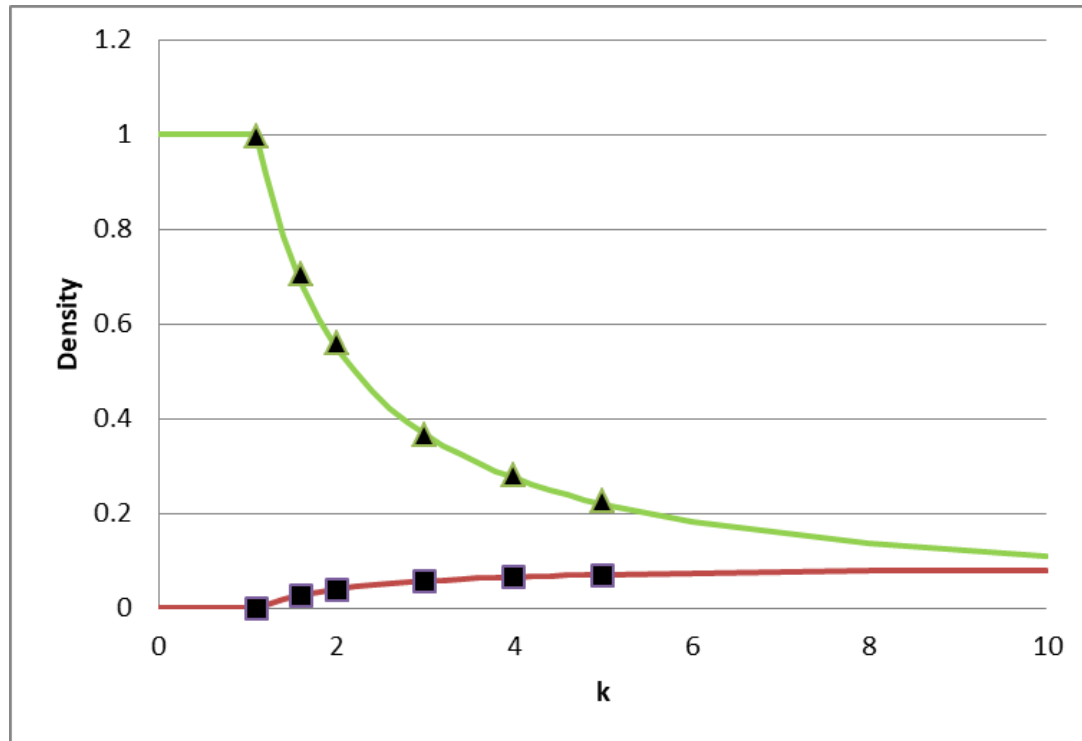
Therefore at the steady state $Y = \dfrac{a - vX}{kX}$.

Putting $X = (v+w)/k$ into this gives $Y = \dfrac{a}{v+w} - \dfrac{v}{k}$.

Summary

Solution 1: X = a/v   Y = 0

Solution 2: $X = (v+w)/k$ $Y = \dfrac{a}{v+w} - \dfrac{v}{k}$. (This applies if Y > 0)

Example with a = v = 0.1 and w = 1
Netlogo simulations (points) match the theory exactly

What does this mean?

To make Y as big as possible, we need

$$Y = \frac{a}{v+w} - \frac{v}{k}.$$

(i) k as big as possible (high infection rate means many infected trees)

(ii) w as small as possible (low virulence means trees live longer and infect more other trees)

The basic reproductive rate of the parasite R_0 is defined as the average number of new infections caused by a single infected individual in a population of uninfected hosts.

Lifetime of an infected tree is 1/(v+w)
Rate of infection per individual is kX, and $X = a/v$ is the density of the uninfected hosts.

Therefore
$$R_0 = \frac{1}{v+w}\frac{ka}{v} = \frac{a}{v}\frac{k}{v(v+w)}$$

Evolution tries to maximize R_0 – this means making k big or w small.

Competition between two strains of an infection

$$\frac{dX}{dt} = a - vX - X(k_1 Y_2 + k_2 Y_2)$$

$$\frac{dY_1}{dt} = Y_1(k_1 X - (v + w_1)) \qquad\qquad R_1 = \frac{a}{v}\frac{k_1}{(v + w_1)}$$

$$\frac{dY_2}{dt} = Y_2(k_2 X - (v + w_2)) \qquad\qquad R_2 = \frac{a}{v}\frac{k_2}{(v + w_2)}$$

Suppose strain 1 is already present. Then we know X = (v+w_1)/k_1

Now add a small amount of strain 2 and ask if it can invade.

$$\frac{dY_2}{dt} = Y_2(k_2 \frac{v + w_1}{k_1} - (v + w_2))$$

The term in brackets is positive if $\qquad \dfrac{k_2}{v + w_2} > \dfrac{k_1}{v + w_1}$

Or in other words, the second strain invades and replaces the first, if $R_2 > R_1$

What does this mean?

$$\frac{k_2}{v + w_2} > \frac{k_1}{v + w_1}$$

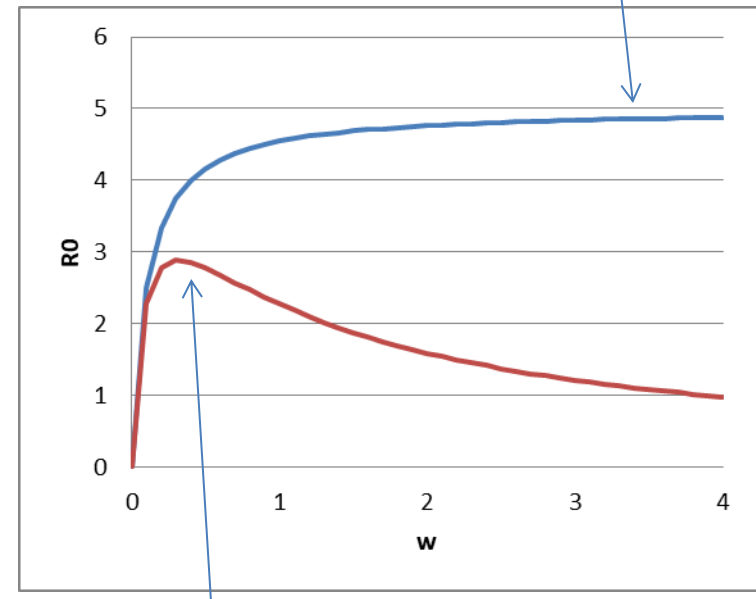If w is fixed, a strain with a higher infectivity will evolve: $k_2 > k_1$
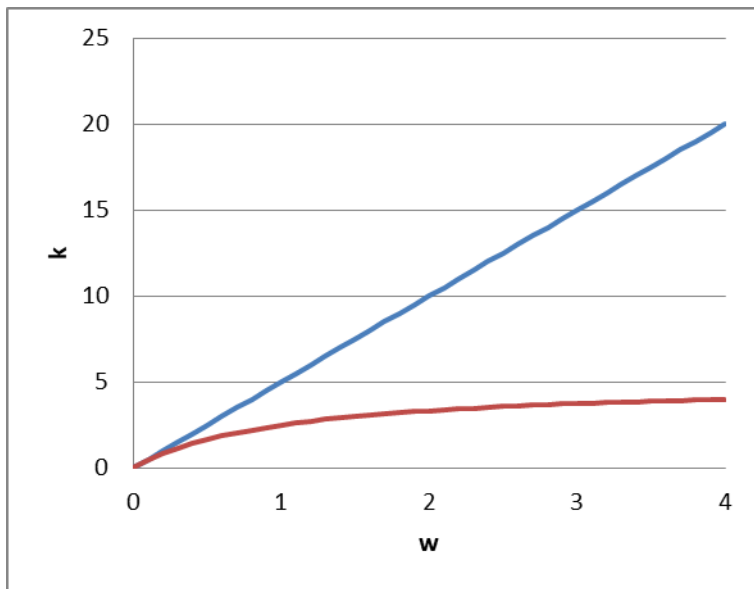
If k is fixed, a strain with a lower virulence will evolve: $w_2 < w_1$

Trade-offs: Suppose infectivity is proportional to virulence $k = \alpha w$
Or suppose k is a saturating function of w:

$$k = \frac{\alpha w}{1 + cw}$$

Evolution towards high virulence will occur

Evolution towards intermediate virulence will occur