

# Vector-borne plant diseases: impact of vector preferences on the spatial spreading of Infectious Diseases

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Joined Work with Prof. F. Hilker and Dr. F. Hamelin



**Food Security** is a Major Challenge around the World.

- Globally, it is estimated that 20-40% of crop yields are lost to pests and diseases.
- In particular, when this loss affects staple crops such as rice, wheat, maize and tubers such as potatoes and sweet potatoes, it directly threatens food security and nutrition.



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Studying Crop-Diseases dynamics in the field is a difficult task.

That is why modeling, analysis, and numerical simulations can be helpful and bring new insights to better focus the experiments and also improve the control strategies.

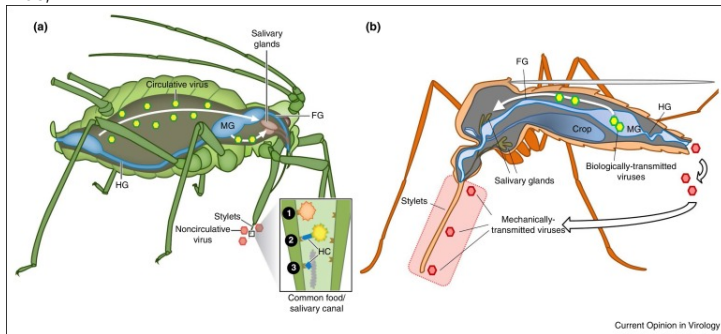


# Introduction

Vector-borne diseases affect humans, animals and also plants

Sap-sucking Insects (plant hosts), like aphids: Potato virus Y, Plum pox virus,..

Mosquito (human and animal hosts)  
Malaria, Dengue, Yellow fever, Zika, ...



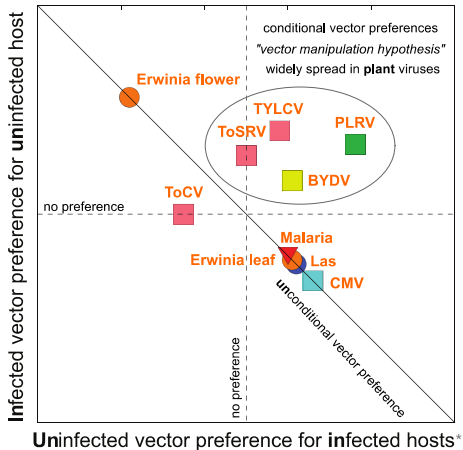
- Most models assume vectors visit hosts randomly
- However, growing evidence shows that many vectors do not visit hosts randomly



\*From Blanc & Gutiérrez (2015) Current Opinion in Virology

# Introduction

Vectors may be differentially attracted towards infected and uninfected hosts, depending on whether they carry the pathogen or not



\*

\*After Gandon (2018) American Naturalist

# A model with vector preferences

Let  $I(x, t)$  be the infected host density at time  $t$  and location  $x \in \mathbb{R}$ , and  $V(x, t)$  and  $U(x, t)$  the infected (viruliferous) and uninfected vector densities, respectively:

$$\begin{aligned}I_t &= bpV \frac{a(N - I)}{a(N - I) + I} - rI, \\V_t &= bqU \frac{ul}{ul + (N - I)} - (m + \delta)V + DV_{xx}, \\U_t &= (m + \delta)V - bqU \frac{ul}{ul + (N - I)} + DU_{xx},\end{aligned}\tag{1}$$

with non negative initial conditions. Biological parameters:

- $N$  the total constant Host population.
- $m$  ( $r$ ) is the vector (host) recovery/mortality rate.
- $D$  the diffusion rate.



# A model with vector preferences

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The epidemiological parameters:

- $b$ : the biting rate
- $p$ : probability of pathogen transmission
- $q$ : probability of pathogen acquisition.
- $1/\delta$ , the virus lifespan (related to non-persistent or semi-persistent viruses),



# A model with vector preferences

$$\begin{aligned}I_t &= bpV \frac{a(N-I)}{a(N-I)+I} - rI, \\V_t &= bqU \frac{uI}{uI+(N-I)} - (m+\delta)V + DV_{xx}, \\U_t &= (m+\delta)V - bqU \frac{uI}{uI+(N-I)} + DU_{xx},\end{aligned}\tag{3}$$

The epidemiological parameters:

- $a$ : preference/attraction of infected vectors for uninfected hosts;
- $u$ : preference of uninfected vectors for infected hosts.





# The diffusion-less model

Let  $W = U + V$  be the total vector population density, then  
 $W_t = DW_{xx}$ .

Assuming  $W(x, 0) = K$  (the vector is established) for all  
 $x \in (-\infty, +\infty)$ , with  $W_t(x, 0) = 0$  for all  $x$ , such that  $W = K$  for  
all  $(x, t) \in \mathbb{R} \times \mathbb{R}_+$ .



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Therefore, since  $U = K - V$ , model (3) reduces to:

$$\begin{aligned} I_t &= bpV \frac{a(N - I)}{a(N - I) + I} - rI, \\ V_t &= bq(K - V) \frac{uI}{uI + (N - I)} - (m + \delta)V + DV_{xx}. \quad (4) \end{aligned}$$



# The diffusion-less model

With the following rescaling

$$\tau = (m + \delta)t, \quad i = \frac{I}{N}, \quad \text{and} \quad v = \frac{V}{K},$$

and setting  $\beta = \frac{bpK}{(m+\delta)N}$ ,  $\rho = \frac{r}{(m+\delta)}$ ,  $\theta = \frac{bq}{(m+\delta)}$ , leads to

$$\begin{aligned} i' &= \beta v \frac{a(1-i)}{a(1-i) + i} - \rho i := f_1(i, v), \\ v' &= \theta(1-v) \frac{ui}{ui + (1-i)} - v := f_2(i, v). \end{aligned} \quad (5)$$



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Since

$$\frac{\partial f_1}{\partial v} \geq 0, \quad \frac{\partial f_2}{\partial i} \geq 0,$$

the system is **Cooperative**: no periodic orbits, and every bounded trajectory converges to an equilibrium (Smith 2008).



$$\begin{aligned}i' &= \beta \frac{a(1-i)}{a(1-i)+i} v - \rho i, \\v' &= \theta \frac{ui}{ui+(1-i)} (1-v) - v.\end{aligned}\tag{6}$$

It is well known that the disease-free equilibrium  $(0, 0)$  is locally asymptotically stable (LAS) if and only if  $\mathcal{R}_0^2 < 1$ , where

$$\mathcal{R}_0^2 = \frac{\beta\theta}{\rho} u = \frac{b^2 pq}{r(m+\delta)} \frac{K}{N} u = \mathcal{R}_{0,1} u.$$

Note that  $\mathcal{R}_0^2$  only depends on  $u$  (the preference of uninfected vectors for infected hosts) and not on  $a$  (the preference of infected vectors for uninfected hosts).



# The temporal model with vector preferences

An endemic equilibrium,  $(i^*, v^*)$ , is solution of the quadratic

$$Q(i^*) = Ai^{*2} + Bi^* + C = 0,$$

in which

$$\begin{aligned} A &= (a - 1)(u(1 + \theta) - 1), \\ B &= \left( (2 - (1 + \theta)u) - \frac{\beta\theta}{\rho}u \right) a - 1 \\ C &= a(\mathcal{R}_0^2 - 1). \end{aligned}$$

We discuss the number of endemic equilibrium according to the cases  $\mathcal{R}_0^2 > 1$ ,  $\mathcal{R}_0^2 = 1$ , and  $\mathcal{R}_0^2 < 1$ .



# The diffusion-less model

- When  $\mathcal{R}_0^2 > 1$ , only one single endemic equilibrium exists.
- When  $\mathcal{R}_0^2 = 1$ , an endemic equilibrium exists iff  $a > 1$  and  $\frac{\alpha\theta}{(1+\theta)\beta} > \frac{a}{a-1} > 1$ .



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- When  $\mathcal{R}_0^2 < 1$ , there exist two biologically endemic equilibria iff the following set of conditions is satisfied:

$$A < 0, \quad B > 0, \quad B^2 - 4AC > 0, \quad 2A + B > 0$$

Otherwise there exists no endemic equilibrium.





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Otherwise there exists no endemic equilibrium.

Setting  $u^* = \frac{1}{1+\theta}$ , necessary conditions for two endemic equilibria to coexist are:

- $a > 1$ : infected vectors prefer uninfected hosts.
- $u < u^* < 1$ : uninfected vectors avoid infected hosts.

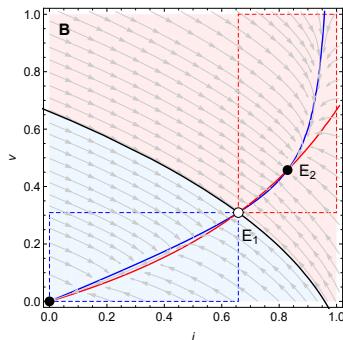
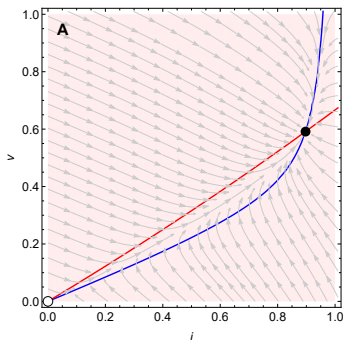


Since our system is Cooperative, we have

## Qualitative analysis

- When  $\mathcal{R}_0^2 < 1$  and  $\mathbf{0}$  is the only equilibrium, then it is GAS.
- When  $\mathcal{R}_0^2 < 1$ , and two positive equilibrium  $E_2$  and  $E_1$  exist, with  $E_1 \ll E_2$ , then  $\mathbf{0}$  and  $E_2$  are LAS, and  $E_1$  is unstable.
- When  $\mathcal{R}_0^2 > 1$ , then the endemic equilibrium  $E$  is GAS, and  $\mathbf{0}$  is unstable.

# The diffusion-less model

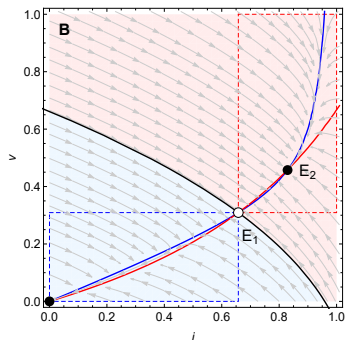
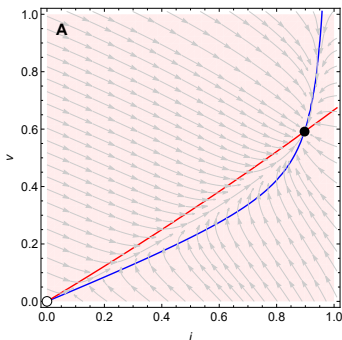


Parameter values:  $a = 15, \beta = 2.5, \rho = 1, \theta = 2$ .

(A)  $\mathcal{R}_0^2 = 1.44 > 1$  ( $u = 0.3$ ): the endemic equilibrium is the only attractor.



# The diffusion-less model



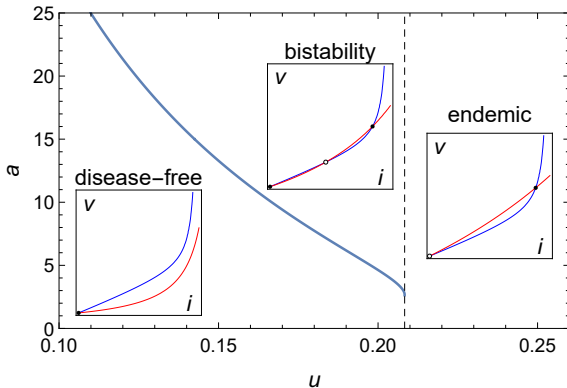
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(A)  $\mathcal{R}_0^2 = 1.44 > 1$  ( $u = 0.3$ ): the endemic equilibrium is the only attractor.

(B) Bistable case:  $\mathcal{R}_0^2 = 0.72 < 1$  ( $u = 0.15$ ).



# Two-parameters bifurcation diagram.



**Figure:** The fold (transcritical) bifurcation curves are shown in solid blue (dashed black). They meet at  $(a \approx 2.663, u \approx 0.2083)$ . The insets are illustrations of the nullcline constellations of the parameter domains leading to different dynamical regimes.

# The diffusion model with vector preferences

We rescale variables and parameters in this way:  $\tau = (m + \delta)t$  and

$$i = \frac{I}{N}, \quad v = \frac{V}{K}, \quad \beta = \frac{bpK}{(m + \delta)N}, \quad \rho = \frac{r}{m + \delta}, \quad \theta = \frac{bq}{m + \delta},$$

and let

$$\xi = x \sqrt{\frac{m + \delta}{D}}.$$

A dimensionless version of model (4) is the following:

$$\begin{aligned} i_\tau &= \beta v \frac{a(1-i)}{a(1-i) + i} - \rho i, \\ v_\tau &= \theta(1-v) \frac{ui}{ui + (1-i)} - v + v_{\xi\xi}, \end{aligned} \quad (7)$$

in which the subscripts denote differentiation with respect to  $\tau$  or  $\xi$ .



# The diffusion model with vector preferences

We consider the following spaces

$$\mathcal{S} = \{(i, v) \mid v \in L^2(\mathbb{R}); i \in L^\infty(\mathbb{R})\},$$

and

$$\mathcal{S}_{1,1} = \{(i, v) \in \mathcal{S} \mid 0 \leq v \leq 1; 0 \leq i \leq 1\}.$$

## Theorem (Existence and uniqueness)

*For any initial values  $(i_0, v_0) \in \mathcal{S}_{1,1}$ , system (7) admits a unique non-negative bounded solution such that*

$$i \in C([0, \infty); L^\infty(\mathbb{R})) \cap C^1([0, \infty); L^\infty(\mathbb{R})),$$

*and*

$$v \in C([0, \infty); L^\infty(\mathbb{R})) \cap C([0, \infty); H^2(\mathbb{R})) \cap C^1([0, \infty); L^2(\mathbb{R})).$$



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According to the temporal model study, it seems relevant to study the existence or not of travelling wave (TW) solutions.





The system **being cooperative and partially degenerate**, it is relatively straightforward to check

- the hypothesis of Theorem 4.2 [Li 2012] to show the existence of a monostable Travelling Wave connecting  $\mathbf{0}$  to  $E$ , the endemic equilibrium, when  $\mathcal{R}_0^2 > 1$
- the hypothesis of Theorem 4.2 [Fang & Zhao 2019], to show the existence of a bistable Travelling Wave solution connecting  $\mathbf{0}$  to  $E$ , the endemic equilibrium, when  $\mathcal{R}_0^2 < 1$ .




# Minimal Speed of the Monostable TW

- We posit that the front speed is linearly determined as given by the minimum possible wave speed based on the linearisation at the leading edge of the wave.
- We apply the minimum wave speed approach (Lewis & Schmitz, 1996; Haderler & Lewis, 2002) to the linearised model for finding the pathogen spreading speed.
- At the leading edge of the front invading the disease-free equilibrium,  $i$  and  $v$  have small positive values. We linearise system (7) at the leading edge:

$$\begin{cases} i_\tau &= \beta v - \rho i, \\ v_\tau &= \theta u i - v + v_{\zeta\zeta} \end{cases}$$

Then, we are looking for TW solutions

$y = (i, v)^T = k \exp(-s(\zeta - c\tau))$ , where  $c$  is the wave speed.  AMAPlab

# Minimal Speed of the Monostable TW

Following the methodology outlined by Hadeler & Lewis (2002), we derive the minimum speed,  $c^*(\rho, \beta\theta u)$ , which is the square root of the largest positive root of the following cubic equation

$$c_3(c^2)^3 + c_2(c^2)^2 + c_1(c^2)^1 + c_0 = 0,$$

with

$$c_3 = 4\beta\theta u + (\rho - 1)^2,$$

$$c_2 = 2\rho^3 + 2\rho^2 + (6\beta\theta u - 8)\rho + 18\theta u\beta + 4,$$

$$c_1 = \rho^4 + 8\rho^3 - (6\beta\theta u + 8)\rho^2 + 36u\rho\beta\theta - 27u^2\beta^2\theta^2,$$

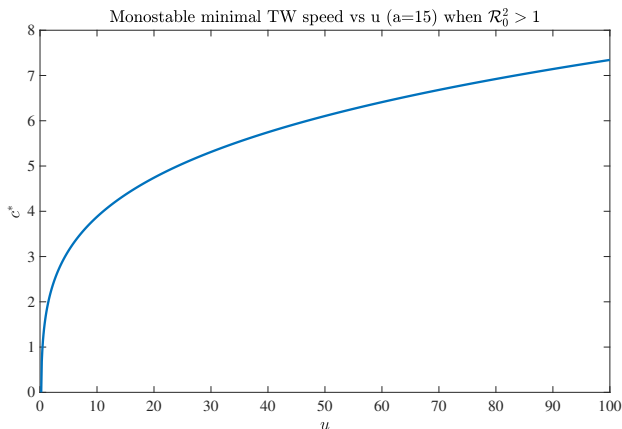
$$c_0 = -4\rho^3(\beta\theta u - \rho) = -4\rho^4(\mathcal{R}_0^2 - 1).$$

Since  $\mathcal{R}_0^2 > 1$ , we have that  $c_0$  is negative and  $c_3$  is positive such that one positive root always exists. Thus the speed depends on  $\beta$  and  $\mathcal{R}_0^2$ , thus on  $u$ , and not on  $a$ .



# Minimal Speed of the Monostable TW

Using the previous result, we can estimate the minimal speed for the monostable wavefront.



However, things are more complex than that!



# Minimal Speed of the Monostable TW

Assuming  $\rho \gg 1$ , we consider a QSSA to reduce our model to

$$v_t \approx \theta(1-v) \frac{ui^\sharp(v)}{ui^\sharp(v) + 1 - i^\sharp(v)} - v + v_{\xi\xi} =: W(v) + v_{\xi\xi}, \quad (8)$$

where  $0 < i^\sharp(v) := \frac{(\frac{\beta}{\rho}v+1)^a - \sqrt{\left(\left(\frac{\beta}{\rho}v-1\right)^2 a + 4\frac{\beta}{\rho}v\right)^a}}{2(a-1)} < 1$ .

Notice that in the monostable case ( $\mathcal{R}_0^2 > 1$ ),  $W(0) = 0$ ,  $W(v^*) = 0$ , and  $W(v) > 0$  for all  $v \in (0, v^*)$ . When

$$\frac{W(v)}{v} < W'(0) \quad \text{for all } v \in (0, v^*), \quad (9)$$

the spreading speed of the wave is linearly determined by

$$c^* = 2\sqrt{W'(0)} = 2\sqrt{\frac{\beta}{\rho}\theta u - 1} = 2\sqrt{\mathcal{R}_0^2 - 1}.$$



# Minimal Speed of the Monostable TW

If (9) is not satisfied, the spreading speed may not be linearly determined. A sufficient condition for condition (9) not to hold is  $W''(0) > 0$ . We have

$$W''(0) = -\frac{2\frac{\beta}{\rho}u\theta \left( (1 + (u-1)a)\frac{\beta}{\rho} + a \right)}{a},$$

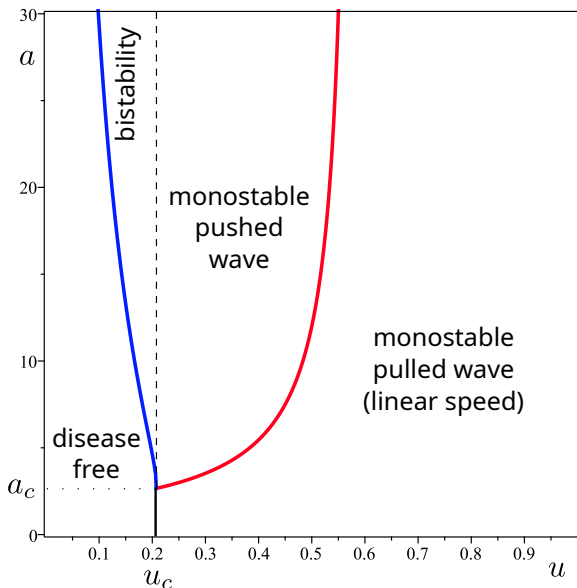
and so  $W''(0) > 0$  is equivalent to

$$(u-1)\frac{\beta}{\rho} + 1 < 0 \quad \text{and} \quad a > \frac{\frac{\beta}{\rho}}{-((u-1)\frac{\beta}{\rho} + 1)} =: \tilde{a}(u). \quad (10)$$

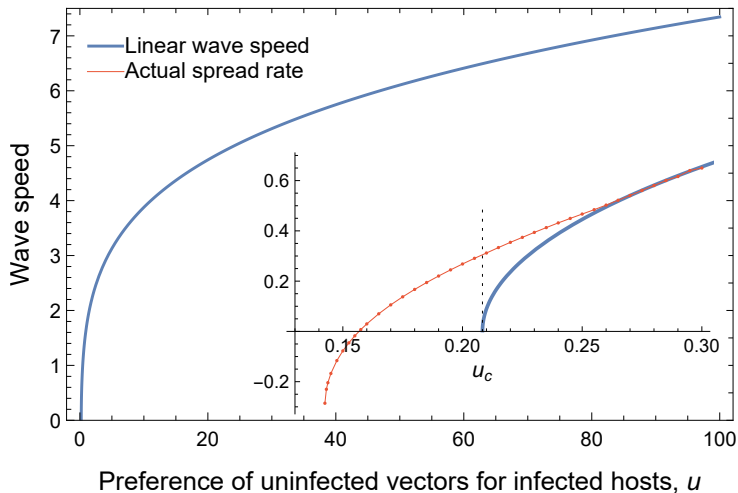
This means that the curve separating pulled waves (linear speed) with pushed waves (nonlinear speed) in the parameter plane “originates” at  $(u_c, a_c)$ , where  $u_c$  is such that  $\mathcal{R}_0(u_c) = 1$ , and  $a_c = \frac{1}{1 - \frac{u_c}{u^*}}$ .



# Minimal Speed of the Monostable TW

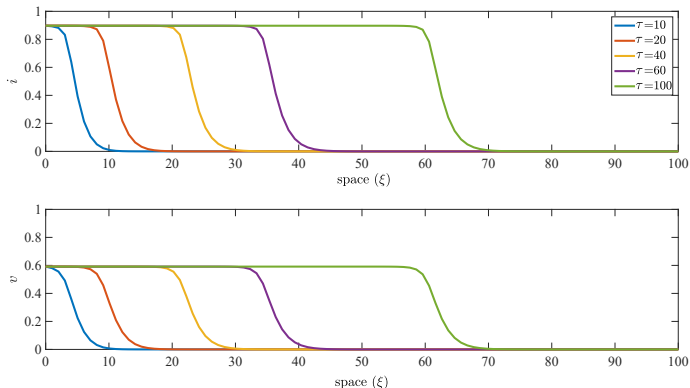


# Minimal Speed of the Monostable TW



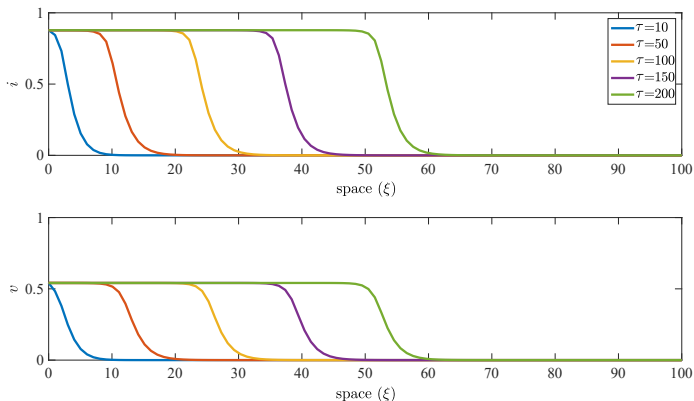


# Simulations of the monostable TW



$\mathcal{R}_0^2 = 1.44 > 1$ , with  $u = 0.3$ . The disease is invading  $c^* > 0$ .

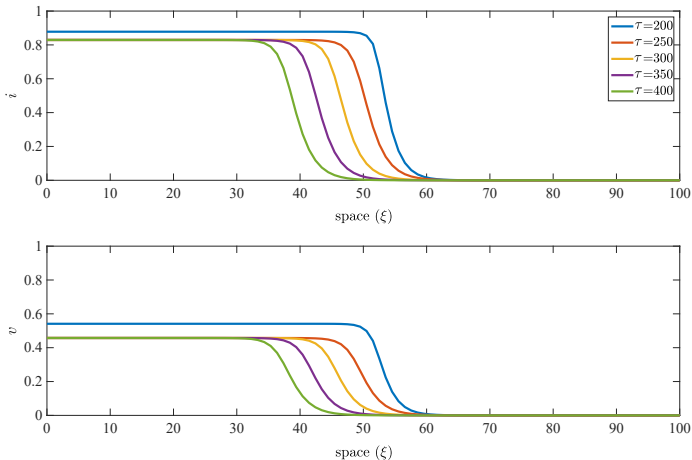
# Simulations of the bistable TW ( $\mathcal{R}_0^2 < 1$ )




$\mathcal{R}_0^2 = 0.96 < 1$ , with  $u = 0.2$ . The disease is invading  $c^* > 0$ .

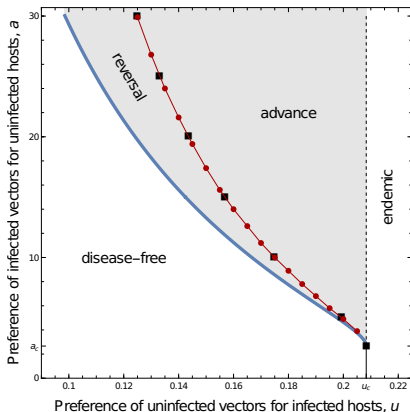


# Simulations of the bistable TW - Front reversal



$\mathcal{R}_0^2 = 0.72 < 1$ , with  $u = 0.15$ . The spread is reversing,  $c^* < 0$ .  AMAPlab

# Two-parameter bifurcation diagram of the TW dynamic



The parameter domains of reversal and advance are separated by a curve corresponding to stalled waves, with zero wave speed, obtained by solving the PDE system (grey square) or the QSSA (red points) for  $\rho = 1$ ,  $\beta = 2.4$  and  $\theta = 2$ .



# Conclusion: Plant Vector-borne diseases

Monostable case ( $\mathcal{R}_0^2 > 1$ ):

- the disease invades the spatial domain
- since  $\mathcal{R}_0^2 = \beta\theta u/\rho$ , the disease spreading speed depends only on  $\rho$  and  $\beta\theta u$ , and does not depend on  $a$ .

**Interpretation:** at the leading edge of the front, close to the disease-free equilibrium, there are so few infected hosts that the preference of infected vectors for uninfected hosts has a negligible effect on the dynamics.

- However, the spreading speed can be non linear and may depend on  $a$ : the disease spread is not driven by the leading edge of the invasion front ("pulled wave"), but by the whole of the front ("pushed wave").



# Conclusion: Plant Vector-borne diseases

Bistable case ( $\mathcal{R}_0^2 < 1$ ):

- the disease either invades or retreats, depending on parameter values: backward bifurcation
- a travelling wave with a negative speed occurs when an endemic equilibrium is replaced by the disease-free one
- front reversal has seldom been shown to occur when bistability is due to the epidemiological dynamics (as opposed to host population dynamics, e.g. Allee effect, see Hilker et al. 2005)



## Outputs

- Vector preferences: VMH and HMH.
- Is it possible to "play" with parameters  $a$  and  $u$ ?
- Roguing the infected plant is an option to get  $\mathcal{R}_0^2 < 1$
- An alternative for modelling vector preference could be density-dependent advection, like "prey-taxis" equation.
- Further improvements are possible: distinguish vegetative and reproductive stages, take into account plant growth.

- New advances in Agronomy, in Forest Sciences, ... will be possible only through multi-disciplinary works that gather researchers from different domains (Mathematicians, computer scientists, software developers, biologists, botanists, agronomists, ...).
- I believe that Maths can bring new insights in Plant/Crop/Forest Science. In other words, Plant Science is really an amazing area to develop and study new Mathematical Problems.
- A need in the developments of **new Mathematical Tools and/or Theories** to study these new problems.





## Thank You!

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### Mathematical Biology



#### Spatial spread of infectious diseases with conditional vector preferences

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## Questions?

