Host mixtures for plant disease control: Benefits from pathogen selection and immune priming

Pauline Clin

Joint work with Frédéric Hamelin,
Frédéric Grognard, Ludovic Mailleret,
and Didier Andrivon.

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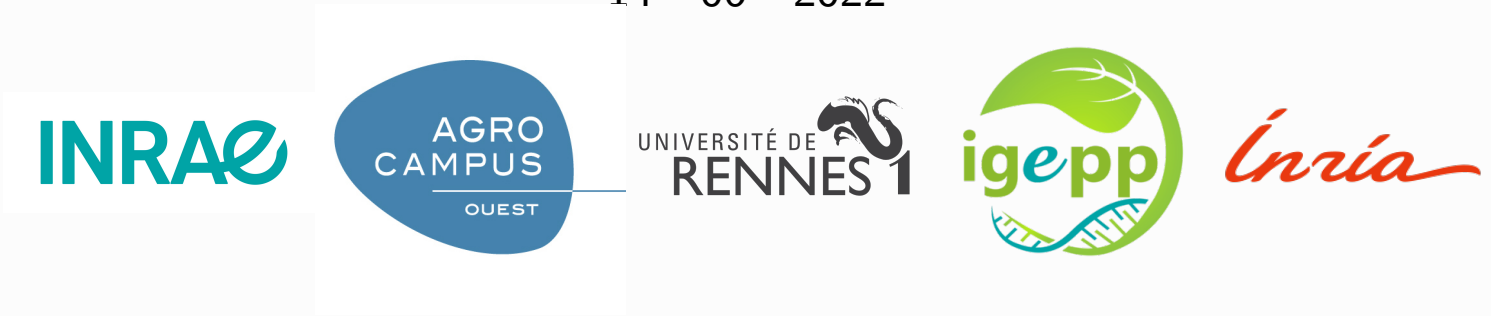

French context

- Pesticide use impacts public health and biodiversity
- Target: halve pesticide use by 2025
- Constraints:
  - Plant breeding for new disease resistance genes
  - Breakdown and durability of resistance

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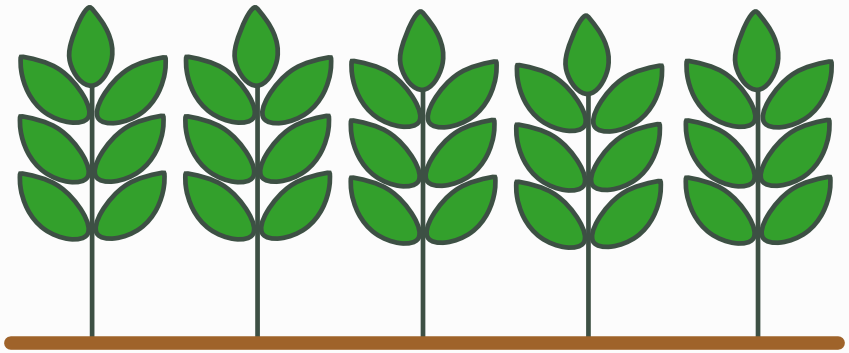
Wanted

New agro-ecological methods

The issue with monocultures



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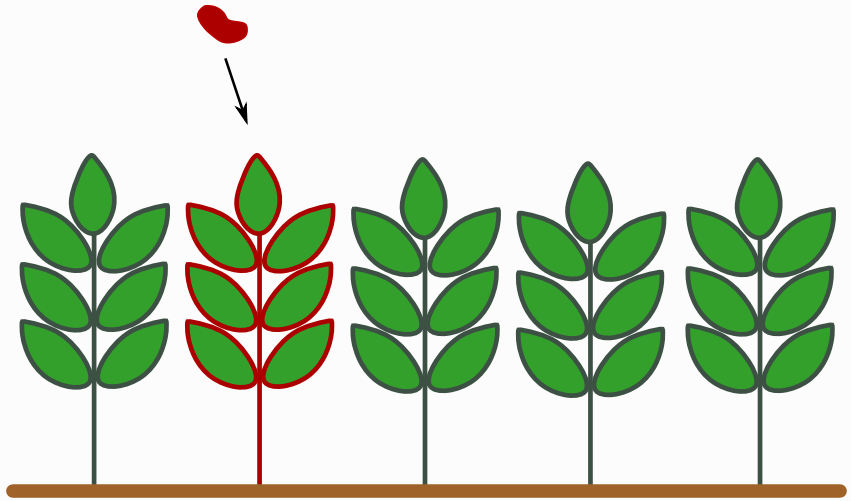

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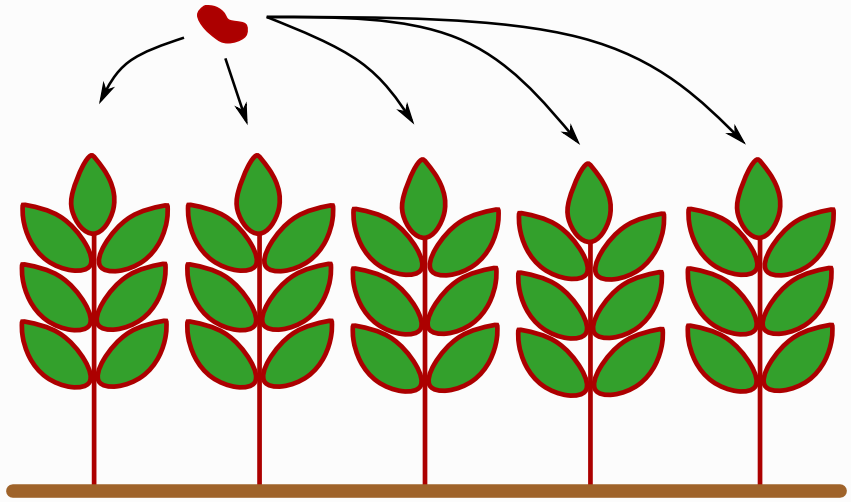
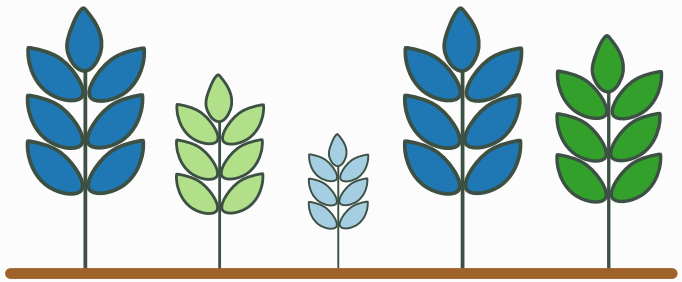
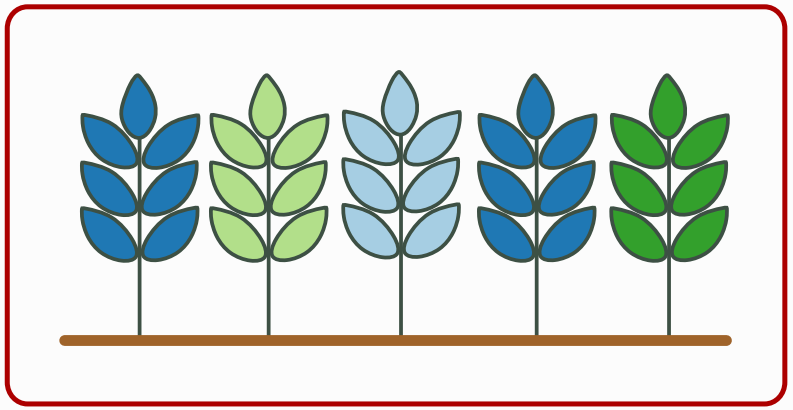


Host mixtures for plant disease control



Cultivar mixture



Multiline

Gene-for-gene interactions

A large part of plant-pathogen interactions are gene-for-gene:

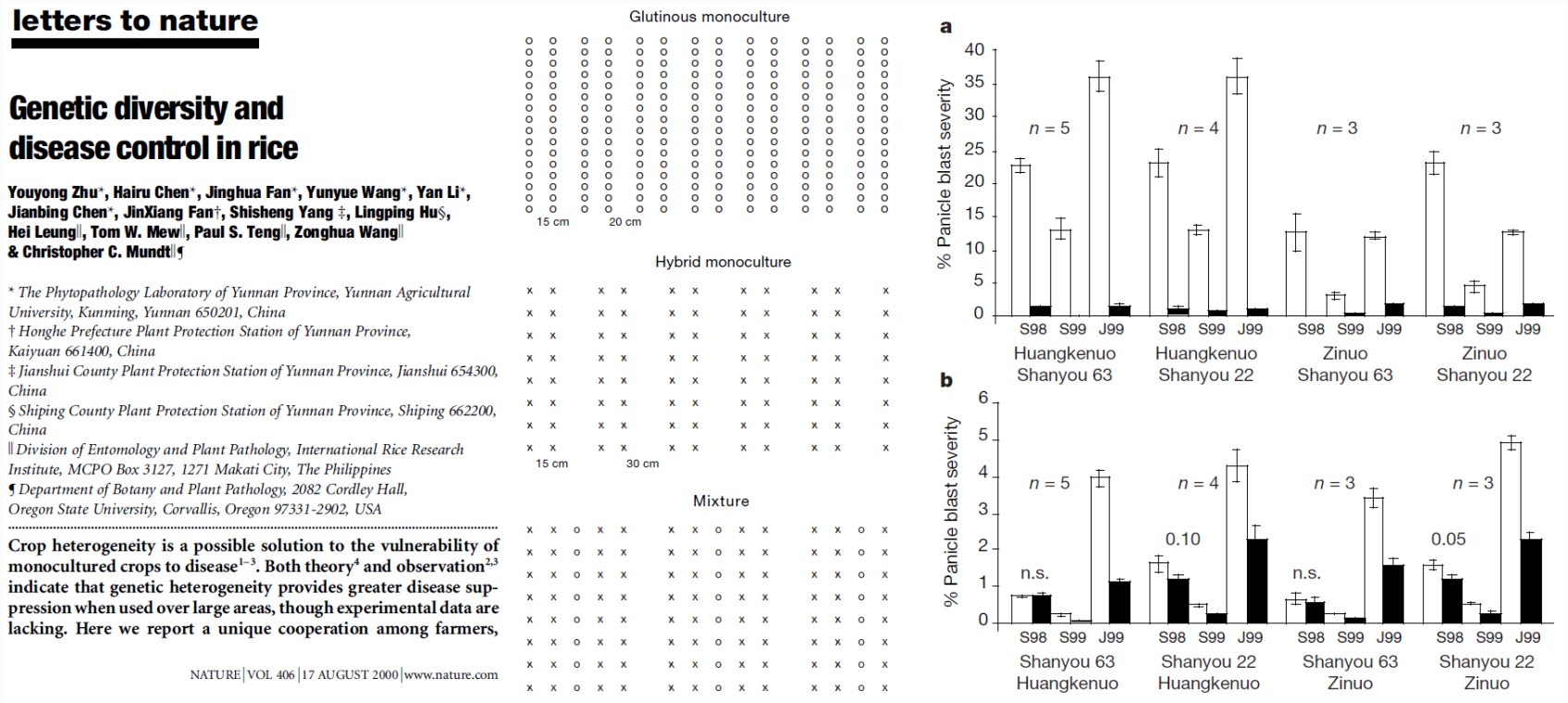
Gene-for-gene interaction matrix

Host \ Pathogen	Avirulent	Virulent
Susceptible	+	+
Resistant	-	+

+ : infection succeeds / − : infection fails

The Yunnan province experimentation (2000)

In mixtures, the prevalence of Rice blast was reduced from 20% to 1% on susceptible varieties compared to susceptible monocultures (dilution effect)



letters to nature

Genetic diversity and disease control in rice

Youyong Zhu*, Hairu Chen*, Jinghua Fan*, Yunyue Wang*, Yan Li*, Jianbing Chen*, JinXiang Fan†, Shisheng Yang ‡, Lingping Hu§, Hei Leung‖, Tom W. Mew‖, Paul S. Teng‖, Zonghua Wang‖ & Christopher C. Mundt‖¶

* The Phytopathology Laboratory of Yunnan Province, Yunnan Agricultural University, Kunming, Yunnan 650201, China
† Honghe Prefecture Plant Protection Station of Yunnan Province, Kaiyuan 661400, China
‡ Jianshui County Plant Protection Station of Yunnan Province, Jianshui 654300, China
§ Shiping County Plant Protection Station of Yunnan Province, Shiping 662200, China
‖ Division of Entomology and Plant Pathology, International Rice Research Institute, MCPO Box 3127, 1271 Makati City, The Philippines
¶ Department of Botany and Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, Oregon 97331-2902, USA

Crop heterogeneity is a possible solution to the vulnerability of monocultured crops to disease[1–3]. Both theory[4] and observation[2,3] indicate that genetic heterogeneity provides greater disease suppression when used over large areas, though experimental data are lacking. Here we report a unique cooperation among farmers,

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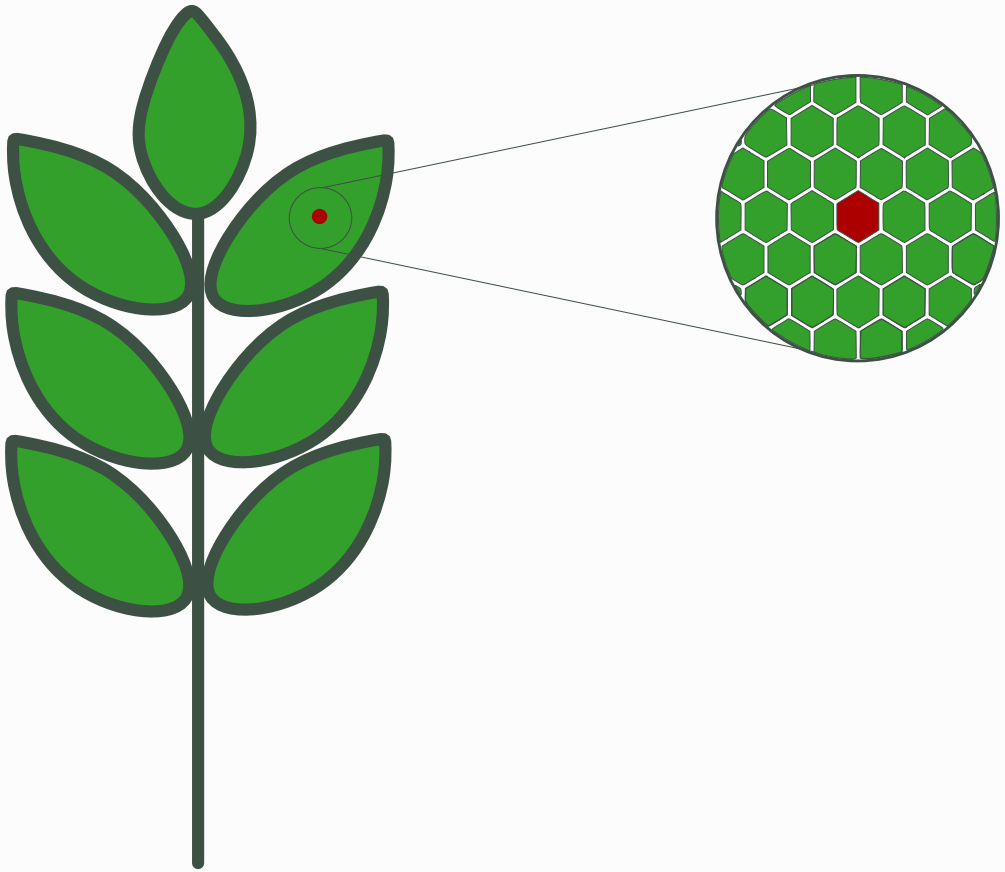
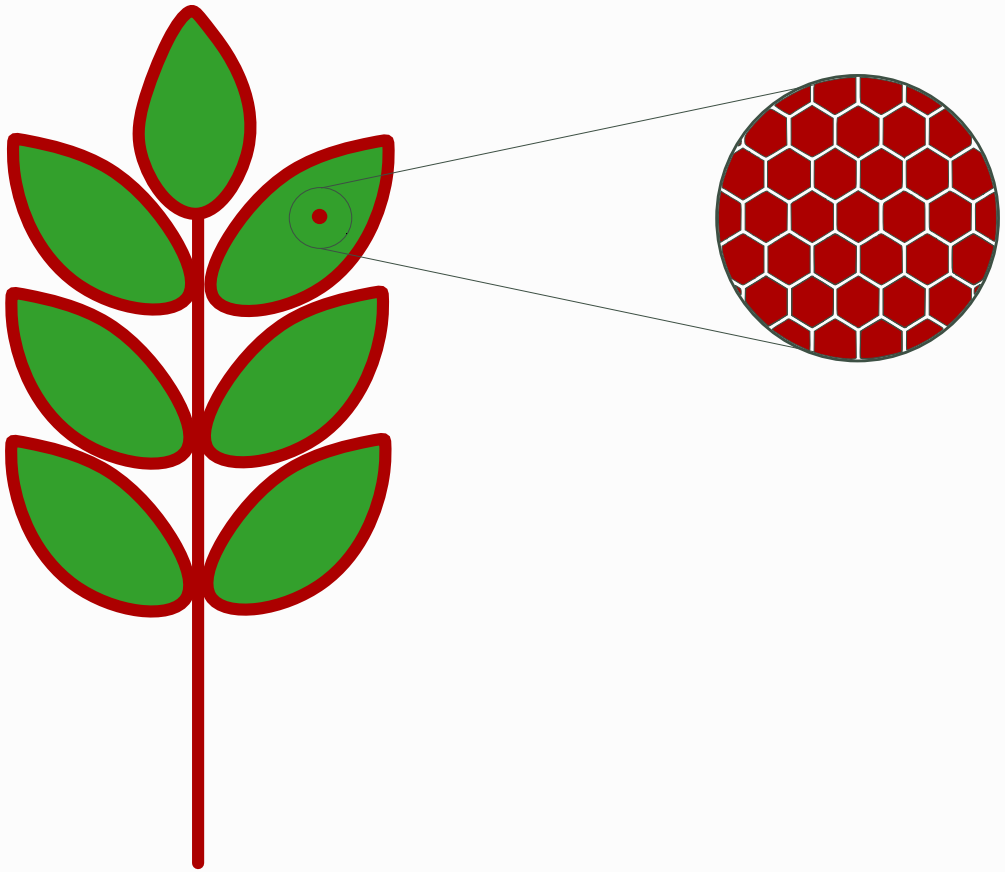
On resistant varieties compared to resistant monocultures, the prevalence decreased from 2% to 1%. Why is that?

Immune response to gene-for-gene interactions



Case of infection success

Immune response to gene-for-gene interactions



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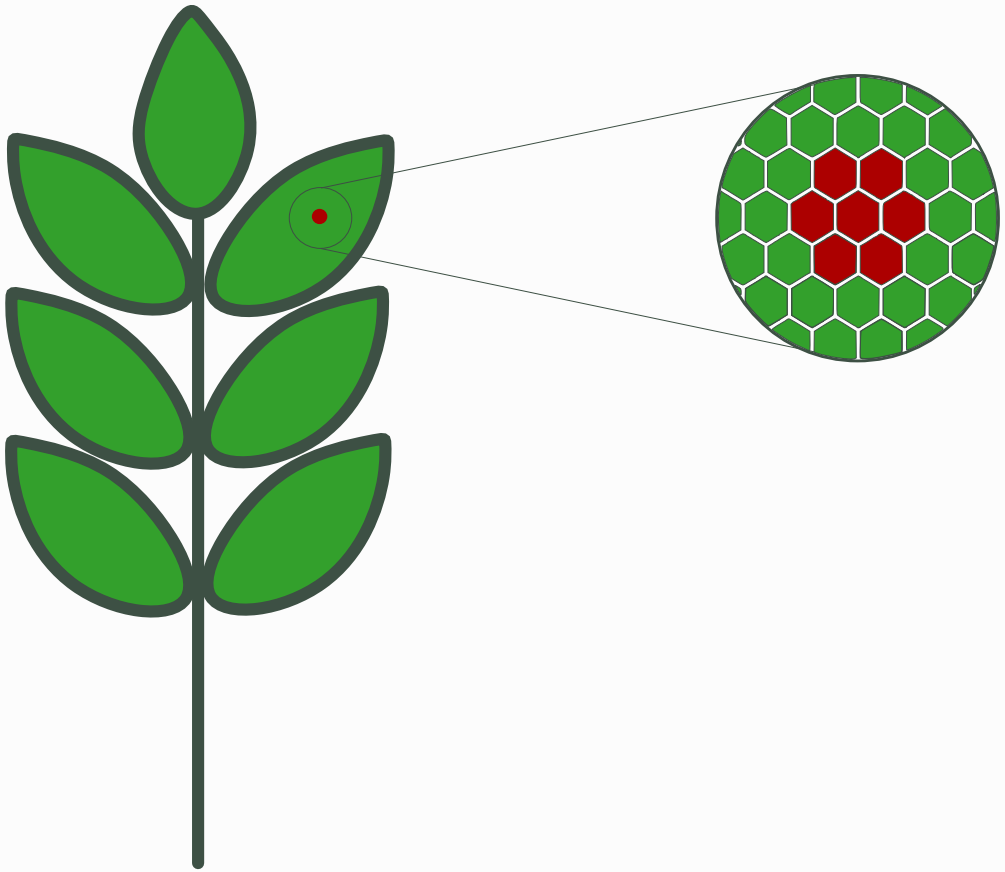
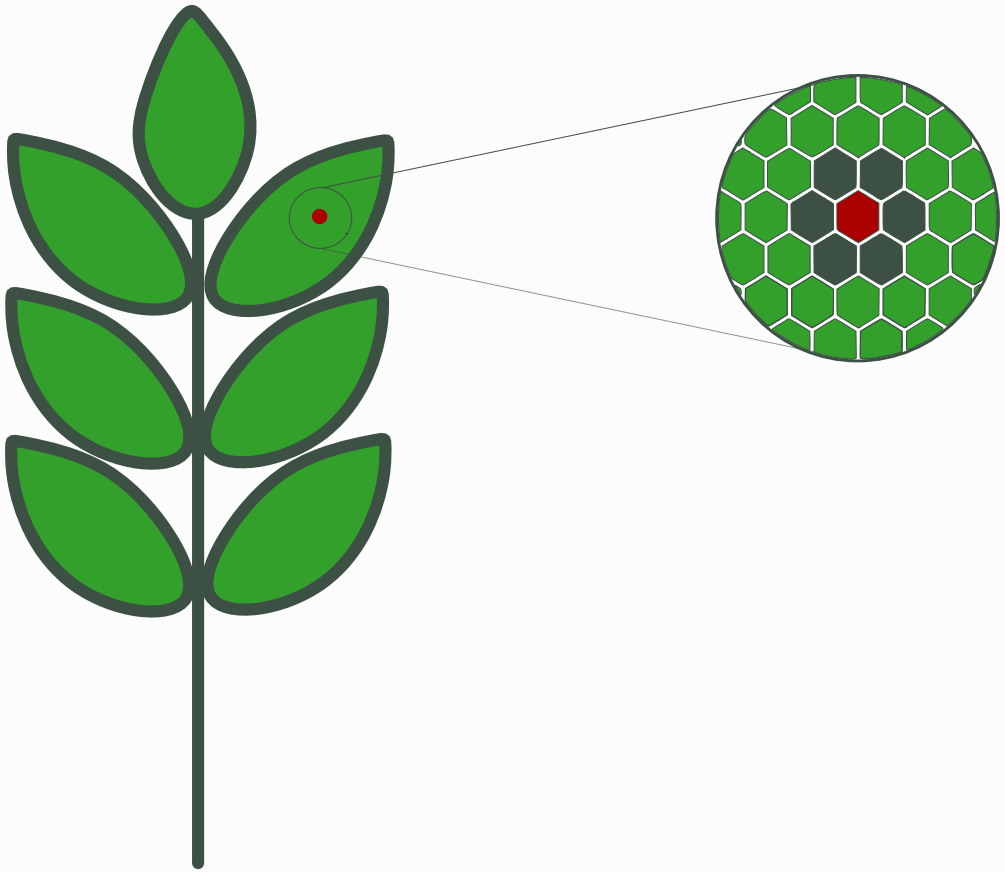


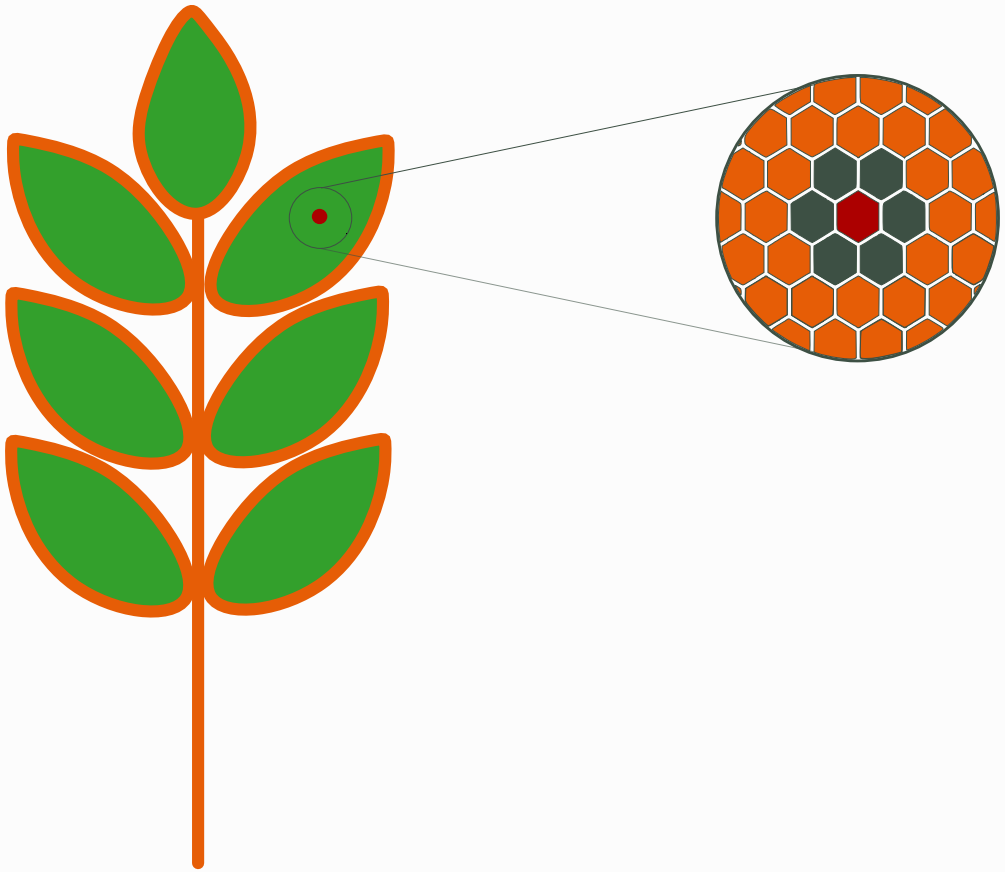
Case of infection failure (avirulent pathogen/resistant plant)

Immune response to gene-for-gene interactions



Case of infection failure → Hypersensitive response

Immune priming



Case of infection failure $\rightarrow$ Systemic acquired resistance

Updated interaction matrix

Taking into account plant immune response:

Gene-for-gene interaction matrix

Host \ Pathogen	Avirulent	Virulent
Susceptible	+	+
Resistant	- but **priming**	+
Primed resistant	-	±

± : infection may not succeed

Mixing n resistant varieties

Mixture with n resistant varieties

- Variety: a plant genotype with a single resistance gene
- For $n = 2$ varieties or loci:

	Pathogen genotypes		
Host genotypes	10	01	11
10	+	**Priming**	+
01	**Priming**	+	+

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Genotypes	Pathogen						
Host	100	010	001	110	101	011	111
100	+	**Priming**	**Priming**	+	+	**Priming**	+
010	**Priming**	+	**Priming**	+	**Priming**	+	+
001	**Priming**	**Priming**	+	**Priming**	+	+	+

Questions

1. Is there **a number of varieties** to use in a mixture **to get rid of** the disease?

2. How much does **priming** improve the mixture efficiency?

Model with $n = 2$ host genotypes

- Each host genotype has a single resistance gene.
- **Virulence complexity k: the number of resistant genes that a pathogen genotype is able to overcome.**

Gene-for-gene interaction matrix (two loci)

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Virulence complexity k	1	1	2

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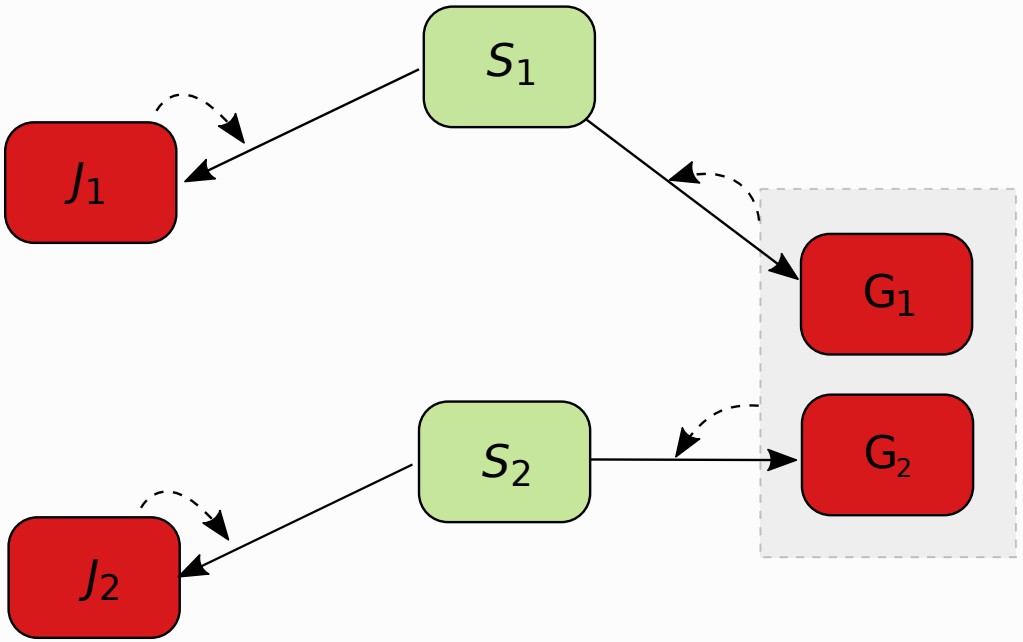
Host genotypes	10	01	11
10	$\boldsymbol{J_1}$	$\boldsymbol{S_1^*}$	$\boldsymbol{G_1}$
01	$\boldsymbol{S_2^*}$	$\boldsymbol{J_2}$	$\boldsymbol{G_2}$
Virulence complexity k	1	1	2

Epidemic model

Based on the previous interaction matrix, for a given resistant host:



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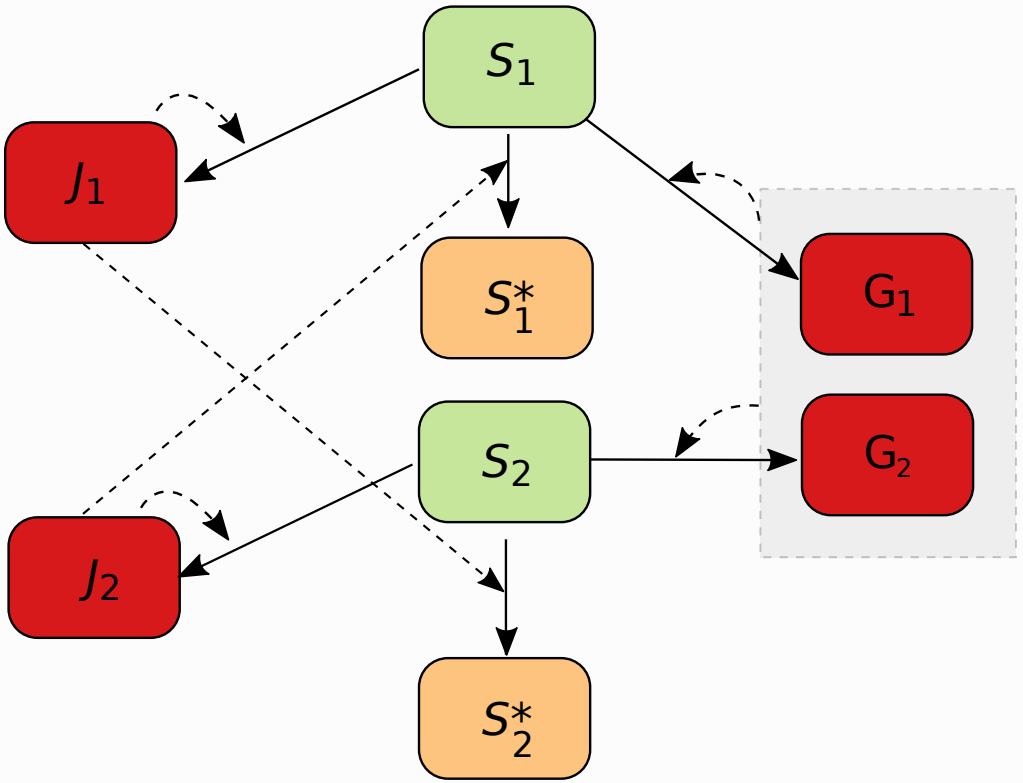

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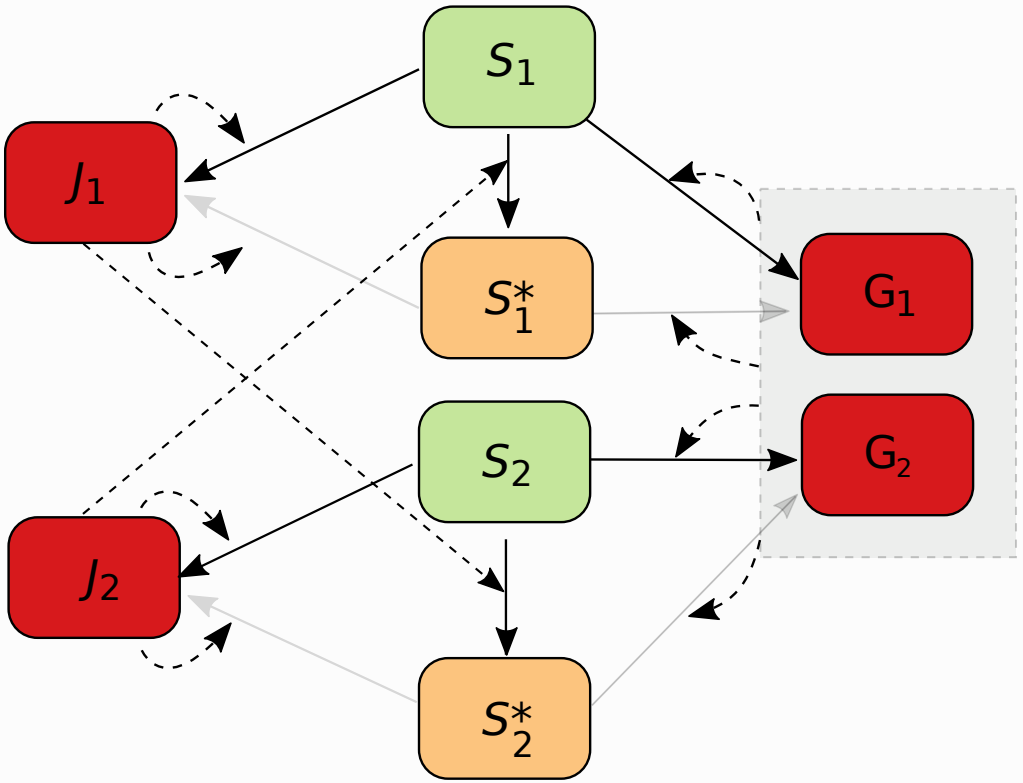

3 important parameters

Basic reproductive number of the pathogen $1 < R = \beta N/\alpha < 500$

Average number of hosts that an infected host can infect **(can take huge values in plant diseases)**.

Frantzen, 2007
Mikaberidze & Mundt, 2016

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Virulence cost $0 < c < 1$

Decreases the fitness of the pathogen genotype bearing virulent gene.

Xanthamonas axonopodis (Wichmann and Bergelson, 2004)
Meloidogyne incognita (Castagnone-Serenoet al, 2007)
Potato virus Y (Janzac et al, 2010)
Phytophtora infestans (Montarry et al, 2010)
Leptosphaeria maculans (Bousset et al, 2018)

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Priming efficiency $0 < \rho < 1$

Reduces the infection success of the virulent pathogen genotype on primed resistant plants.

Tobacco mosaic virus (Ross, 1961)
Full priming efficiency (Kuc, 1982)
A. thaliana (Maleck et al., 2000)

Model for $n = 2$ host genotypes

System in dimensions $n(1 + 2^{n-1}) = 6$:

$$
\begin{aligned}
\dot{S}_1^* &= (1-c)\beta J_2 S_1 - (1-\rho)\beta S_1^* \left((1-c)J_1 + (1-c)^2(G_1+G_2)\right) - (\gamma+\alpha)S_1^* \,, \\
\dot{S}_2^* &= (1-c)\beta J_1 S_2 - (1-\rho)\beta S_2^* \left((1-c)J_2 + (1-c)^2(G_1+G_2)\right) - (\gamma+\alpha)S_2^* \,, \\
\dot{J}_1 &= (1-c)\beta J_1 \left(S_1 + (1-\rho)S_1^*\right) - \alpha J_1 \,, \\
\dot{J}_2 &= (1-c)\beta J_2 \left(S_2 + (1-\rho)S_2^*\right) - \alpha J_2 \,, \\
\dot{G}_1 &= (1-c)^2\beta (G_1+G_2) \left(S_1 + (1-\rho)S_1^*\right) - \alpha G_1 \,, \\
\dot{G}_2 &= (1-c)^2\beta (G_1+G_2) \left(S_2 + (1-\rho)S_2^*\right) - \alpha G_2 \,.
\end{aligned}
$$

Multiplicative fitness cost $\rightarrow (1-c)^k$

where k is the virulence complexity

Model for $n = 3$ host genotypes

For 3 host genotypes:

Gene-for-gene interaction matrix (3 loci)

Genotypes	Pathogen						
Host	100	010	001	110	101	011	111
100	+	**Priming**	**Priming**	+	+	**Priming**	+
010	**Priming**	+	**Priming**	+	**Priming**	+	+
001	**Priming**	**Priming**	+	**Priming**	+	+	+
Virulence complexity k	1	1	1	2	2	2	3

Model for 3 host genotypes

System in dimensions $n(1+2^{n-1}) = 15$:

$$
\begin{aligned}
S_1^{*\prime} &= (1-c)\beta(I_2+I_3)S_{r1} + (1-c)^2\beta(J_{2,3}+J_{3,2})S_{r1} - (1-\rho)(1-c)\beta I_1 S_1^* \\
&\quad -(1-\rho)(1-c)^2\beta(J_{1,2}+J_{2,1})S_1^* - (1-\rho)(1-c)^2\beta(J_{1,3}+J_{3,1})S_1^* \\
&\quad -(1-\rho)(1-c)^3\beta(G_1+G_2+G_3)S_1^* - (\gamma+\alpha)S_1^*\,, \\
S_2^{*\prime} &= (1-c)\beta(I_1+I_3)S_{r2} + (1-c)^2\beta(J_{1,3}+J_{3,1})S_{r2} - (1-\rho)(1-c)\beta I_2 S_2^* \\
&\quad -(1-\rho)(1-c)^2\beta(J_{1,2}+J_{2,1})S_2^* - (1-\rho)(1-c)^2\beta(J_{2,3}+J_{3,2})S_2^* \\
&\quad -(1-\rho)(1-c)^3\beta(G_1+G_2+G_3)S_2^* - (\gamma+\alpha)S_2^*\,, \\
S_3^{*\prime} &= (1-c)\beta(I_1+I_2)S_{r3} + (1-c)^2\beta(J_{1,2}+J_{2,1})S_{r2} - (1-\rho)(1-c)\beta I_3 S_3^* \\
&\quad -(1-\rho)(1-c)^2\beta(J_{1,3}+J_{3,1})S_3^* - (1-\rho)(1-c)^2\beta(J_{2,3}+J_{3,2})S_3^* \\
&\quad -(1-\rho)(1-c)^3\beta(G_1+G_2+G_3)S_3^* - (\gamma+\alpha)S_3^*\,, \\
I_1' &= (1-c)\beta I_1 S_{r1} + (1-\rho)(1-c)\beta I_1 S_1^* - \alpha I_1\,, \\
I_2' &= (1-c)\beta I_2 S_{r2} + (1-\rho)(1-c)\beta I_2 S_2^* - \alpha I_2\,, \\
I_3' &= (1-c)\beta I_3 S_{r3} + (1-\rho)(1-c)\beta I_3 S_3^* - \alpha I_3\,, \\
J_{1,2}' &= (1-c)^2\beta(J_{1,2}+J_{2,1})S_{r1} + (1-\rho)(1-c)^2\beta(J_{1,2}+J_{2,1})S_1^* - \alpha J_{1,2}\,, \\
J_{1,3}' &= (1-c)^2\beta(J_{1,3}+J_{3,1})S_{r1} + (1-\rho)(1-c)^2\beta(J_{1,3}+J_{3,1})S_1^* - \alpha J_{1,3}\,, \\
J_{2,1}' &= (1-c)^2\beta(J_{1,2}+J_{2,1})S_{r2} + (1-\rho)(1-c)^2\beta(J_{1,2}+J_{2,1})S_2^* - \alpha J_{2,1}\,, \\
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J_{3,1}' &= (1-c)^2\beta(J_{3,1}+J_{1,3})S_{r3} + (1-\rho)(1-c)^2\beta(J_{3,1}+J_{1,3})S_3^* - \alpha J_{3,1}\,, \\
J_{3,2}' &= (1-c)^2\beta(J_{3,2}+J_{2,3})S_{r3} + (1-\rho)(1-c)^2\beta(J_{3,2}+J_{2,3})S_3^* - \alpha J_{3,2}\,, \\
G_1' &= (1-c)^3\beta(G_1+G_2+G_3)S_{r1} + (1-\rho)(1-c)^3\beta(G_1+G_2+G_3)S_1^* - \alpha G_1\,, \\
G_2' &= (1-c)^3\beta(G_1+G_2+G_3)S_{r2} + (1-\rho)(1-c)^3\beta(G_1+G_2+G_3)S_2^* - \alpha G_2\,, \\
G_3' &= (1-c)^3\beta(G_1+G_2+G_3)S_{r3} + (1-\rho)(1-c)^3(G_1+G_2+G_3)S_3^* - \alpha G_3\,.
\end{aligned}
$$

Model for an arbitrary number n of varieties

Assumptions:

- All resistant plant genotypes present in the same proportion: $1/n$
- All pathogen diversity initially present: $2^n - 1$ genotypes
- Symmetry assumptions: same virulence cost c and reproductive number R for each pathogen genotypes
- All pathogen genotypes have the same initial prevalence

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The system is in dimension $n+1$ for a focal host genotype: for $k = 1, \ldots, n$,

$$\begin{aligned} m' &= XP - (1-\rho)mF - \nu m, \\ x_k' &= f_k \left(X + (1-\rho)m\right) - x_k \,, \end{aligned}$$

where

m : density of primed hosts for the focal host genotype,

x_k : density of hosts of the focal host genotype infected by a single pathogen genotype with virulence complexity k.

At most one complexity persists at equilibrium

$$x_k' = x_k \left(\phi_k \left(\frac{1}{n} - \rho m - \sum_{i=1}^{n} \binom{n-1}{i-1} x_i \right) - 1 \right)$$

$\rightarrow$ either $x_k = 0$ or $(\cdots) = 0$ at equilibrium,

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Three types of equilibria:

- $(0, 0, 0, 0)$: **Disease-free** equilibrium
- $(\hat{m}, 0, .., 0, \hat{x}_k, 0, .., 0)$: $\boldsymbol{n-1}$ equilibria
- $(0, .., 0, \hat{x}_n)$: **Generalist only** equilibrium

At most one complexity persists at equilibrium

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Competitive exclusion principle

Stability of the $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m}_k)$ equilibrium

$$J = \begin{pmatrix}
\frac{\phi_1}{\phi_k} - 1 & 0 & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & 0 \\
0 & \ddots & \ddots & & & & & & \vdots \\
\vdots & \ddots & \ddots & \ddots & & & & & \vdots \\
0 & \ldots & 0 & \frac{\phi_{k-1}}{\phi_k} - 1 & 0 & \ldots & \ldots & \ldots & 0 \\
-\binom{n-1}{0}\phi_k x_k & \ldots & \ldots & -\binom{n-1}{k-2}\phi_k x_k & -\binom{n-1}{k-1}\phi_k x_k & -\binom{n-1}{k}\phi_k x_k & \ldots & -\binom{n-1}{n-1}\phi_k x_k & -\phi_k x_k \rho \\
0 & \ldots & \ldots & \ldots & 0 & \frac{\phi_{k+1}}{\phi_k} - 1 & 0 & \ldots & 0 \\
\vdots & & & & & \ddots & \ddots & \ddots & \vdots \\
0 & \ldots & \ldots & \ldots & \ldots & \ldots & 0 & \frac{\phi_n}{\phi_k} - 1 & 0 \\
* & * & * & * & J_{n+1,k} & * & * & * & J_{n+1,n+1}
\end{pmatrix}$$

Stability of the $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m}_k)$ equilibrium

$$J = \begin{pmatrix}
\frac{\phi_1}{\phi_k} - 1 & 0 & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & 0 \\
0 & \ddots & \ddots & & & & & & \vdots \\
\vdots & \ddots & \ddots & \ddots & & & & & \vdots \\
0 & \ldots & 0 & \frac{\phi_{k-1}}{\phi_k} - 1 & 0 & \ldots & \ldots & \ldots & 0 \\
-\binom{n-1}{0}\phi_k x_k & \ldots & \ldots & -\binom{n-1}{k-2}\phi_k x_k & -\binom{n-1}{k-1}\phi_k x_k & -\binom{n-1}{k}\phi_k x_k & \ldots & -\binom{n-1}{n-1}\phi_k x_k & -\phi_k x_k \rho \\
0 & \ldots & \ldots & \ldots & 0 & \frac{\phi_{k+1}}{\phi_k} - 1 & 0 & \ldots & 0 \\
\vdots & & & & & \ddots & \ddots & \ddots & \vdots \\
0 & \ldots & \ldots & \ldots & \ldots & \ldots & 0 & \frac{\phi_n}{\phi_k} - 1 & 0 \\
* & * & * & * & J_{n+1,k} & * & * & * & J_{n+1,n+1}
\end{pmatrix}$$

$$\downarrow$$

$$\tilde{J} = \left(\begin{array}{ccccccccc|cc}
\frac{\phi_1}{\phi_k} - 1 & 0 & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & & \ldots & 0 \\
0 & \ddots & \ddots & & & & & & & & \vdots \\
\vdots & \ddots & \ddots & \ddots & & & & & & & \vdots \\
\vdots & & \ddots & \frac{\phi_{k-1}}{\phi_k} - 1 & \ddots & & & & & & \vdots \\
\vdots & & & \ddots & \frac{\phi_n}{\phi_k} - 1 & \ddots & & & & & \vdots \\
\vdots & & & & \ddots & \frac{\phi_{k+1}}{\phi_k} - 1 & \ddots & & & & \vdots \\
\vdots & & & & & \ddots & \ddots & \ddots & & & \vdots \\
0 & \ldots & \ldots & \ldots & \ldots & \ldots & 0 & \frac{\phi_{n-1}}{\phi_k} - 1 & & 0 & 0 \\
\hline
-\binom{n-1}{0}\phi_k x_k & \ldots & \ldots & -\binom{n-1}{k-2}\phi_k x_k & -\binom{n-1}{n-1}\phi_k x_k & -\binom{n-1}{k}\phi_k x_k & \ldots & \ldots & & -\binom{n-1}{k-1}\phi_k x_k & -\phi_k x_k \rho \\
* & * & * & * & * & * & * & * & & J_{n+1,k} & J_{n+1,n+1}
\end{array}\right)$$

Stability $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m}_k)$ equilibrium

The Jacobian matrix $\tilde{J}$ has the following form

$$\tilde{J} = \begin{pmatrix} D_1 & 0 \\ * & B \end{pmatrix}$$

Stability $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m}_k)$ equilibrium

The Jacobian matrix $\tilde{J}$ has the following form

$$\tilde{J} = \begin{pmatrix} D_1 & 0 \\ * & B \end{pmatrix}$$

The stability conditions are defined using the determinant and the trace of the sub-matrix B, and the eigenvalues of the matrix D which are its diagonal terms: for all $i = 1, \ldots, n$ such that $i \neq k$,

$$\lambda_i = \frac{\phi_i}{\phi_k} - 1$$

Stability $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m}_k)$ equilibrium

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The $(0, \ldots, 0, \bar{x}_k, 0, \ldots, 0, \bar{m})$ equilibrium is locally asymptotically stable if and only **if $\phi_k > \phi_i$ for all $i = 1, \ldots, n$ such that $i \neq k$.**

At most one complexity persists at equilibrium

$$x'_k = x_k \left(\phi_k \left(\frac{1}{n} - \rho m - \sum_{i=1}^{n} \binom{n-1}{i-1} x_i \right) - 1 \right)$$

$\rightarrow$ either $x_k = 0$ or $(\cdots) = 0$ at equilibrium, but no two $(\cdots)$ can be equal to 0 simultaneously.

Three types of equilibria:

- $(0, 0, 0, 0)$: **Disease-free** equilibrium
- $(\hat{m}, 0, .., 0, \hat{x}_k, 0, .., 0)$: $\boldsymbol{n-1}$ equilibria
- $(0, .., 0, \hat{x}_n)$: **Generalist only** equilibrium

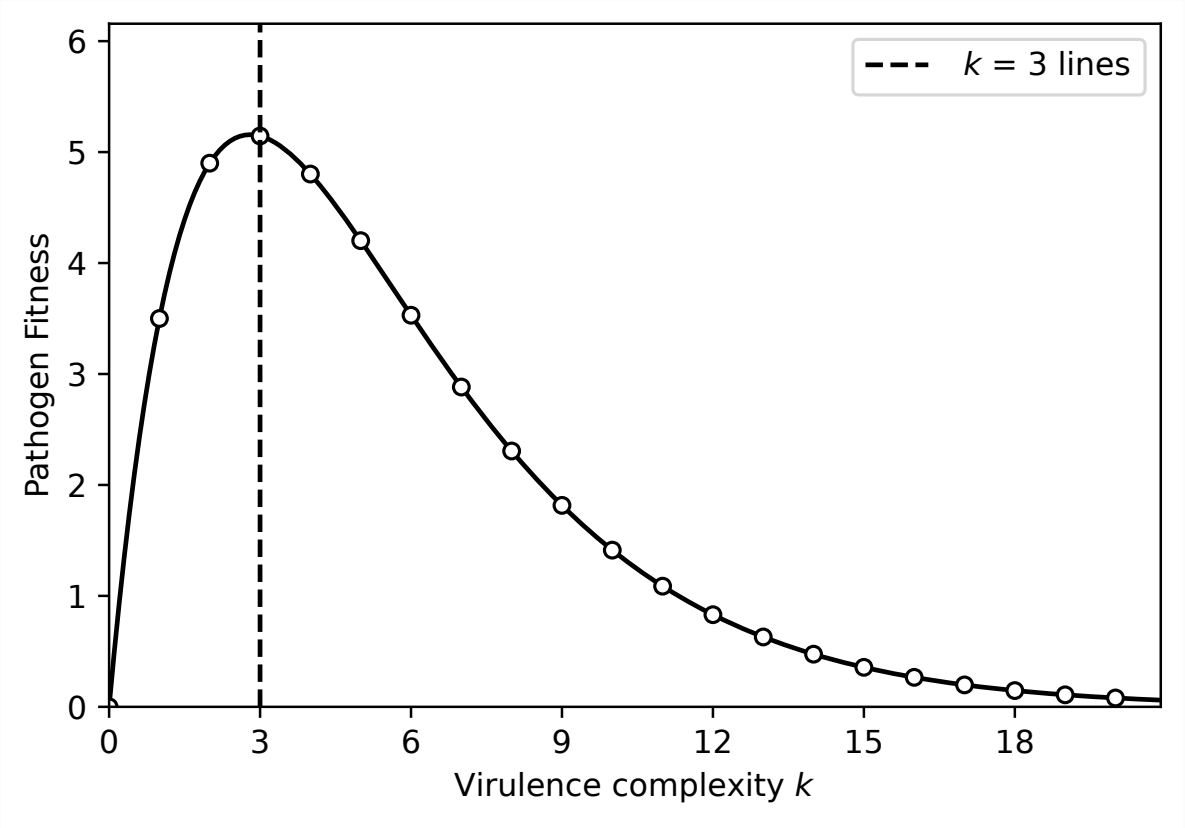
A **single equilibrium is asymptotically stable**, the one containing $\hat{x}_k$ that **maximizes** $\boldsymbol{\phi_k = R(1-c)^k k}$**.**

Competitive exclusion principle

One virulence complexity maximizes the pathogen fitness

There is a virulence complexity k^* that maximizes the fitness:

$$\phi_k = R(1-c)^k k$$



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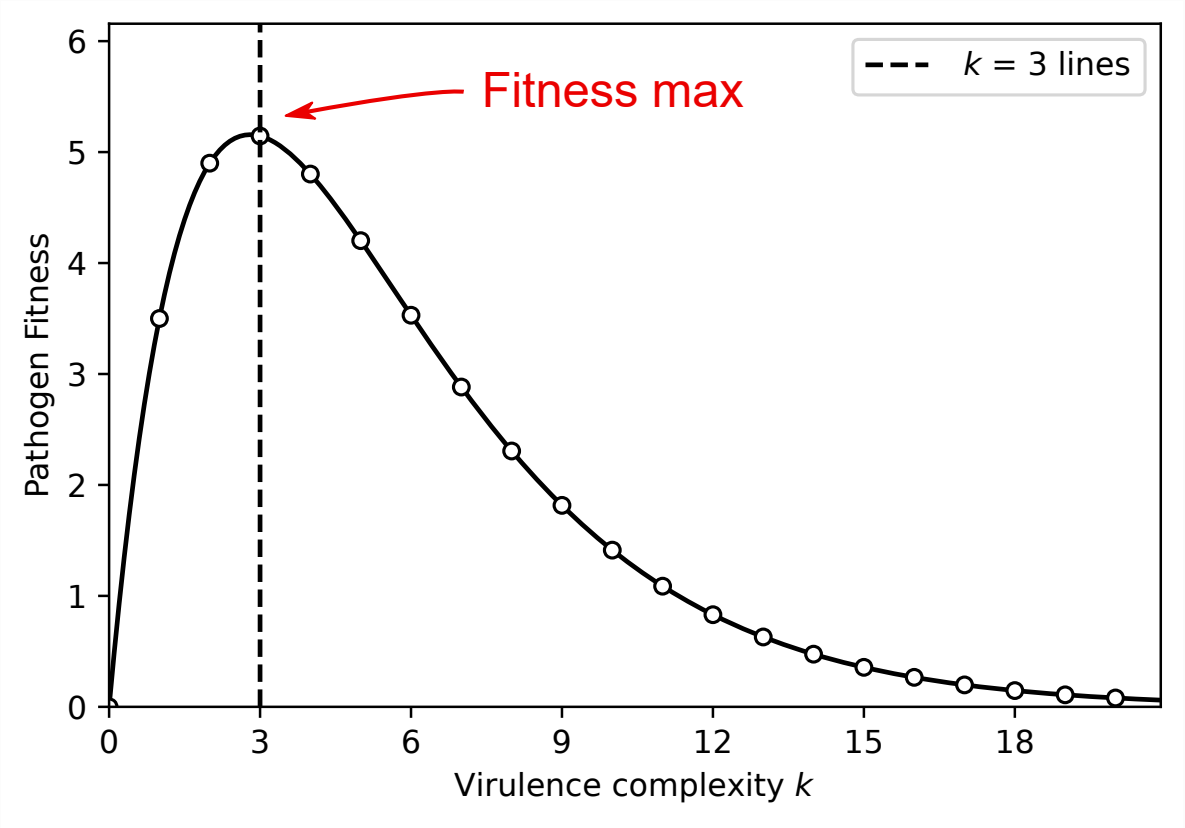
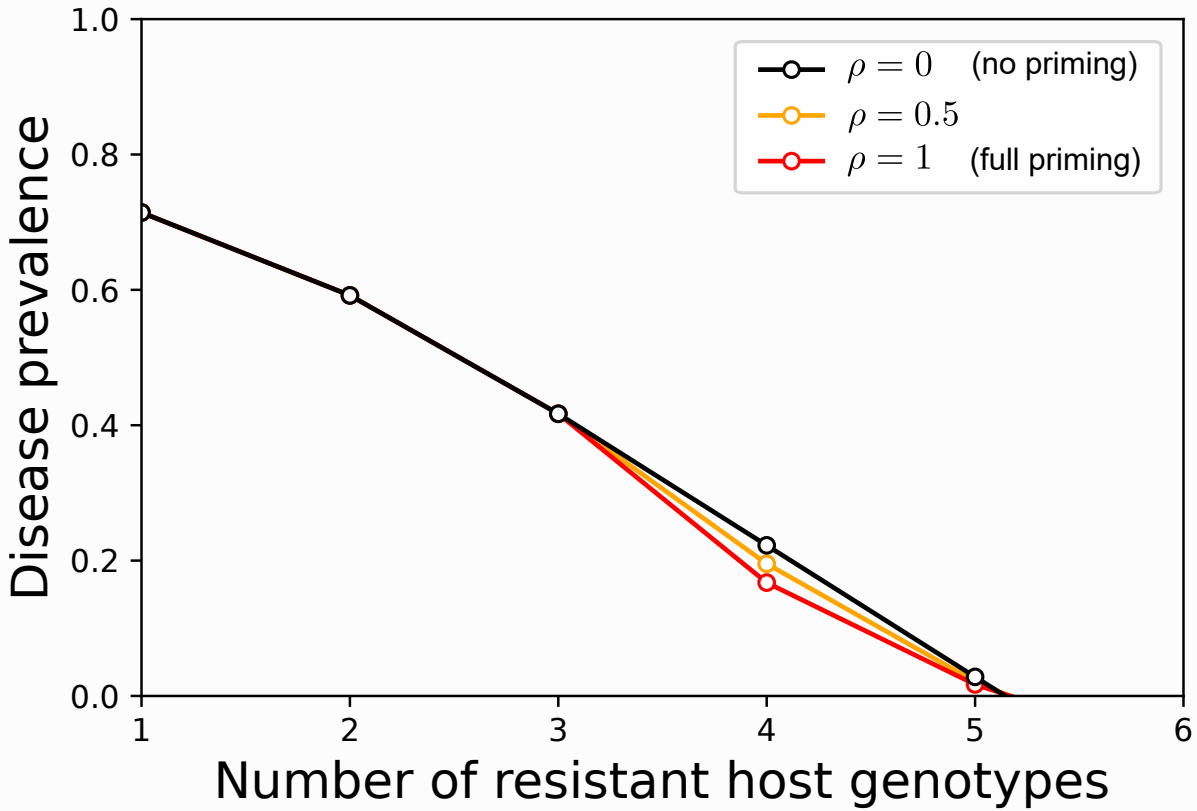


Threshold number of varieties to get rid of the disease

Prevalence of the disease, $P = \binom{n}{k} k x_k$.

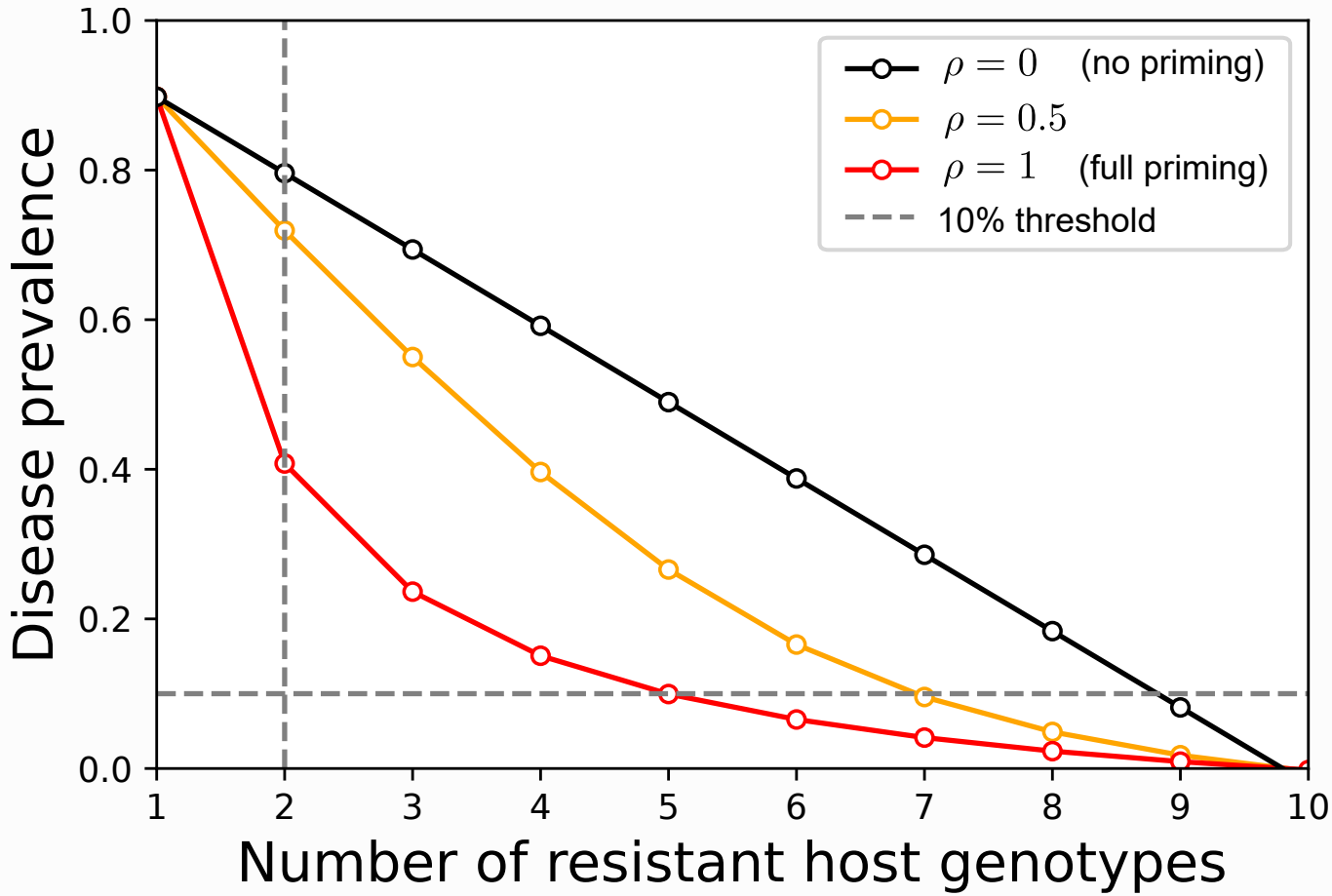


Threshold number of varieties

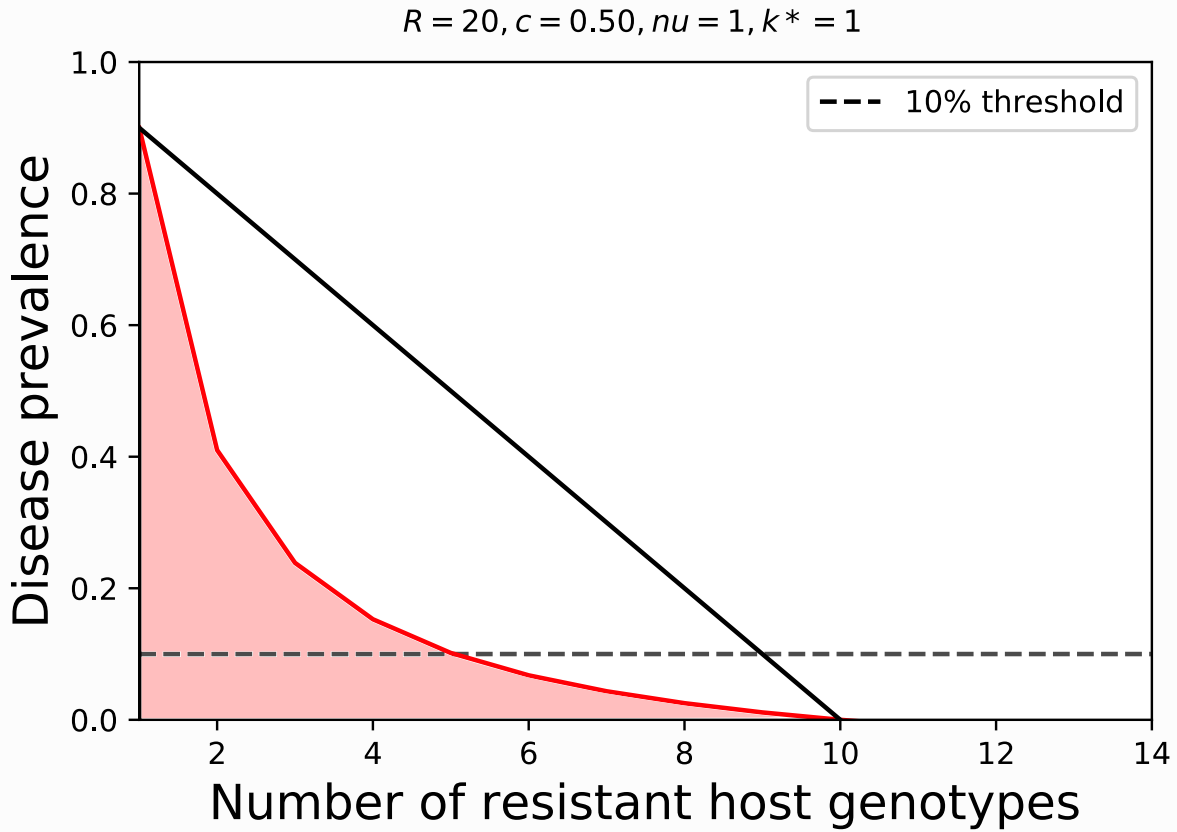
$$n_c = \frac{R}{-\log(1-c)\,\mathrm{e}}$$

Priming effect on mixtures efficiency

Prevalence of the disease, $P = \binom{n}{k} k x_k$.

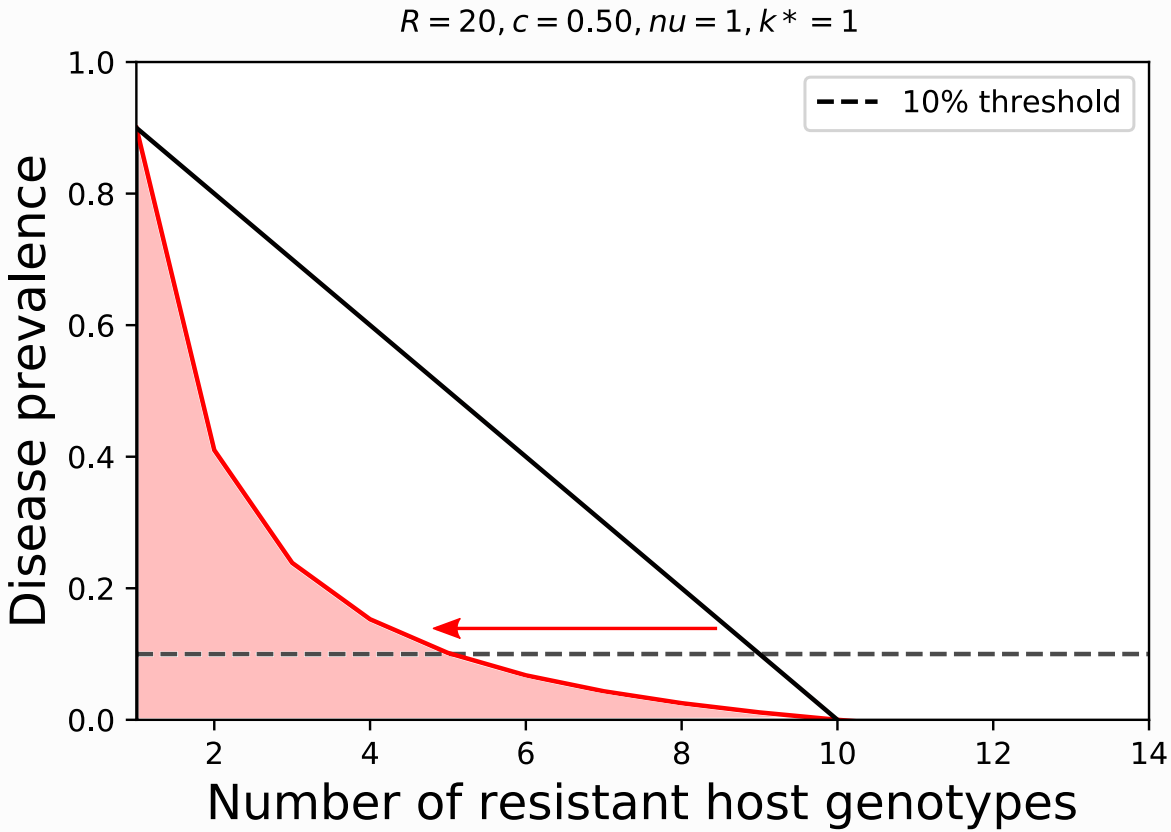


Take-Home Messages



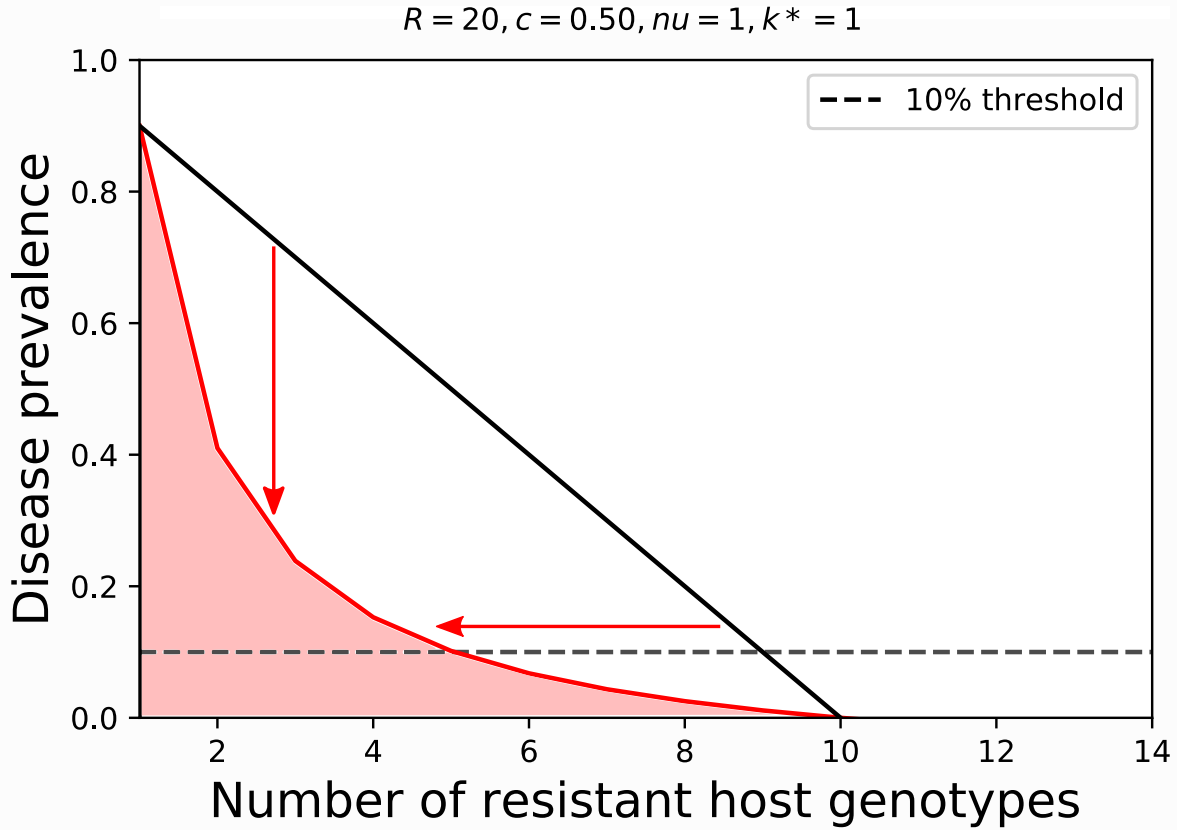
- Threshold number of host genotypes to get rid of the disease

Take-Home Messages



- Threshold number of host genotypes to get rid of the disease
- Priming reduces the number of varieties to be used

Take-Home Messages



- Threshold number of host genotypes to get rid of the disease
- Priming reduces the number of varieties to be used
- Even for a small number of varieties, priming strongly reduces the disease prevalence

Thank you for you attention! Questions ?

Clin, P., Grognard, F., Andrivon, D., Mailleret, L. & Hamelin, F. M. (2022). Host mixtures for plant disease control: benefits from pathogen selection and immune priming. Accepted in Evolutionary Applications.

`https://share.streamlit.io/paulineclin/multiresistance_priming_model/main/app.py`

Binomial coefficients

- $\binom{n-1}{k-1}$: The number of pathogen genotypes of virulence complexity k capable of infecting the focal genotype. This is because a pathogen genotype of complexity k that infects the focal host genotype can also infect $k-1$ host genotypes among the $n-1$ non-focal host genotypes $\rightarrow$ **Infection**
- $\binom{n-1}{k}$: The number of pathogen genotypes of complexity k and able to prime the focal host genotype ($n-1$ since we disregard pathogen genotypes capable of infecting the focal host genotype) $\rightarrow$ **Priming**
- $\binom{n}{k}$: The number of pathogen genotypes of complexity k having infected the focal host genotype $\rightarrow$ **Prevalence**

Existence of equilibria

If $x_k > 0$ for $k \in \{1, \cdots, n\}$, there is $x_k' = 0$ if

$$X + (1-\rho)m = \frac{1}{\phi_k}\,.$$

Theorem: There can be at most one complexity that persists at equilibrium.

Proof (by contradiction): Assume there exists an equilibirum such that at least 2 complexities, $j, k = 1, .., n$, can persist. That means:

$$X_j > 0 \text{ and } X_k > 0.$$

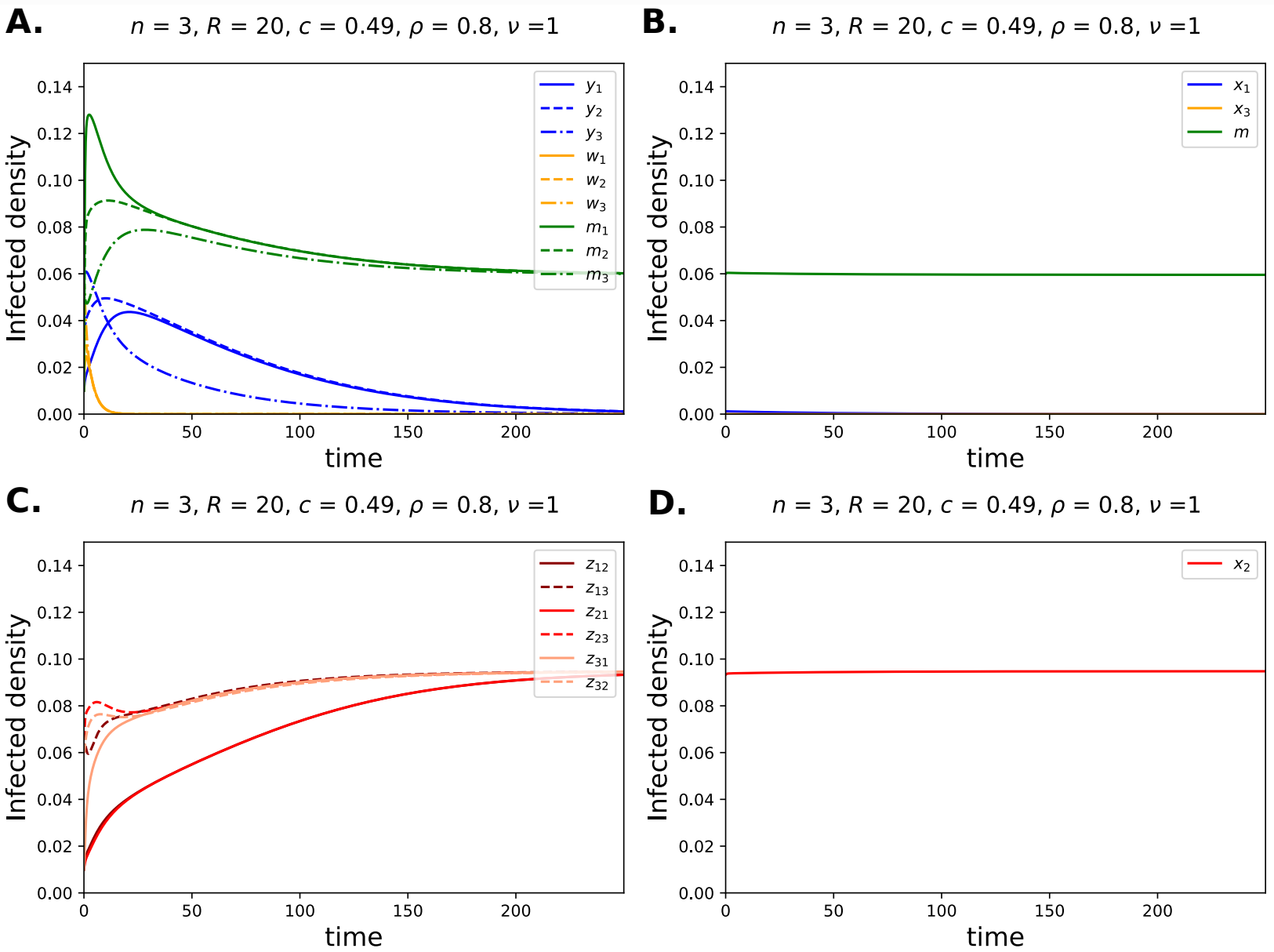
$X_j > 0$ implies $X + (1-\rho)m = 1/\phi_j$,
$X_k > 0$ implies $X + (1-\rho)m = 1/\phi_k$,

This is impossible unless $\phi_j = \phi_k$, which is a non-generic case (biologically irrelevant).

Therefore, the model is simplified as

$$\begin{aligned} m' &= X\binom{n-1}{k}\phi_k x_k - (1-\rho)m\binom{n-1}{k-1}\phi_k x_k - \nu m\,, \\ x_k' &= x_k\left(\phi_k(X + (1-\rho)m) - 1\right)\,. \end{aligned}$$

Convergence of virulence complexity



Stability Disease-free equilibrium $(0, \ldots, 0)$

The Jacobian matrix of size $(n+1) \times (n+1)$ is

$$J = \begin{pmatrix} \frac{\phi_1}{n} - 1 & 0 & \ldots & \ldots & 0 \\ 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \ldots & 0 & \frac{\phi_n}{n} - 1 & 0 \\ \frac{\binom{n-1}{1}\phi_1}{n} & \ldots & \frac{\binom{n-1}{n-1}\phi_{n-1}}{n} & 0 & -\nu \end{pmatrix}$$

Triangular matrix $\rightarrow$ the eigenvalues are its **diagonal elements**: for all $i = 1, ..., n$,

$$\begin{aligned} \lambda_i &= \frac{\phi_i}{n} - 1\,, \\ \lambda_{n+1} &= -\nu < 0\,. \end{aligned}$$

The Disease-free equilibrium $(0, \ldots, 0)$ is locally asymptotically stable if and only if the pathogen fitness $\phi_i < n$ **for all** $i = 1, \ldots, n$.

Stability of the $(0, \ldots, 0, \bar{x}_n, 0)$ equilibrium

The jacobian matrix is

$$J = \left(\begin{array}{ccccc|cc} \frac{\phi_1}{\phi_n} - 1 & 0 & \ldots & \ldots & 0 & 0 & 0 \\ 0 & \ddots & \ddots & & \vdots & \vdots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots & \vdots & \vdots \\ \vdots & & \ddots & \ddots & 0 & \vdots & \vdots \\ 0 & \ldots & \ldots & 0 & \frac{\phi_{n-1}}{\phi_n} - 1 & 0 & 0 \\ \hline -\binom{n-1}{0}\phi_n x_n & \ldots & \ldots & \ldots & -\binom{n-1}{n-2}\phi_n x_n & \phi_n(\frac{1}{n} - 2x_n) - 1 & -\phi_n x_n \rho \\ \binom{n-1}{1}\frac{\phi_1}{\phi_n} & \ldots & \ldots & \ldots & \binom{n-1}{n-1}\frac{\phi_n}{\phi_n} & 0 & -(1-\rho)\phi_n x_n - \nu \end{array}\right)$$

and has the following form

$$J = \begin{pmatrix} D_2 & 0 \\ * & T \end{pmatrix}$$

J is a block triangular matrix, and its eigenvalues are the eigenvalues of D_2 and T, i.e. the diagonal terms.

Stability of the $(0, \ldots, 0, \bar{x}_n, 0)$ equilibrium

Therefore, the eigenvalues are: for all $i = 1, \ldots, n-1$,

$$\begin{aligned} \lambda_i &= \frac{\phi_i}{\phi_n} - 1\,, \\ \lambda_n &= \phi_n \left(\frac{1}{n} - 2x_n \right) - 1\,, \\ \lambda_{n+1} &= -(1-\rho)\phi_n x_n - \nu < 0\,. \end{aligned}$$

The $(0, \ldots, 0, \bar{x}_n, 0)$ equilibrium is locally asymptotically stable if and only if $\phi_n > \phi_i$ for all $i = 1, \ldots, n-1$.

Cooperative systems

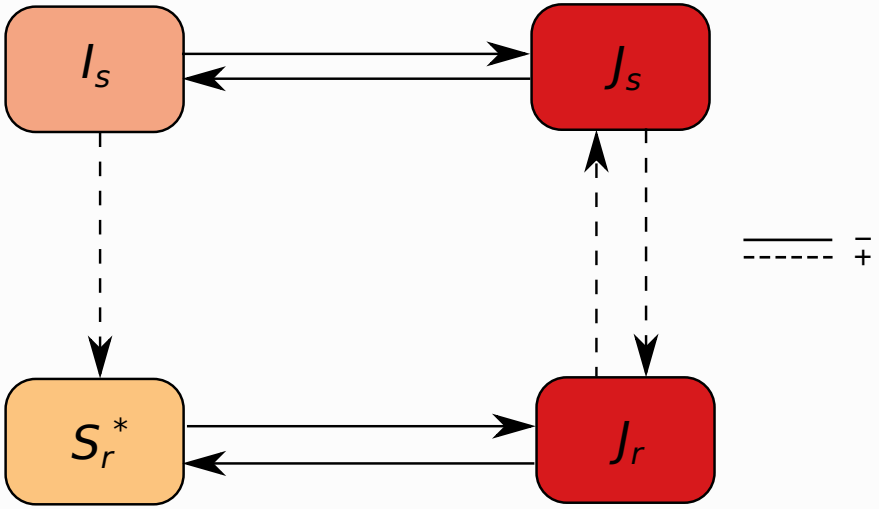
Hal Smith, 2008 ; Hirsch, 1989

Conditions

- Positive interactions between variables,
- Irreducible jacobian matrix.

Jacobian matrix

$$J = \begin{pmatrix} * & 0 & - & 0 \\ + & * & 0 & - \\ - & 0 & * & + \\ 0 & - & + & * \end{pmatrix}$$



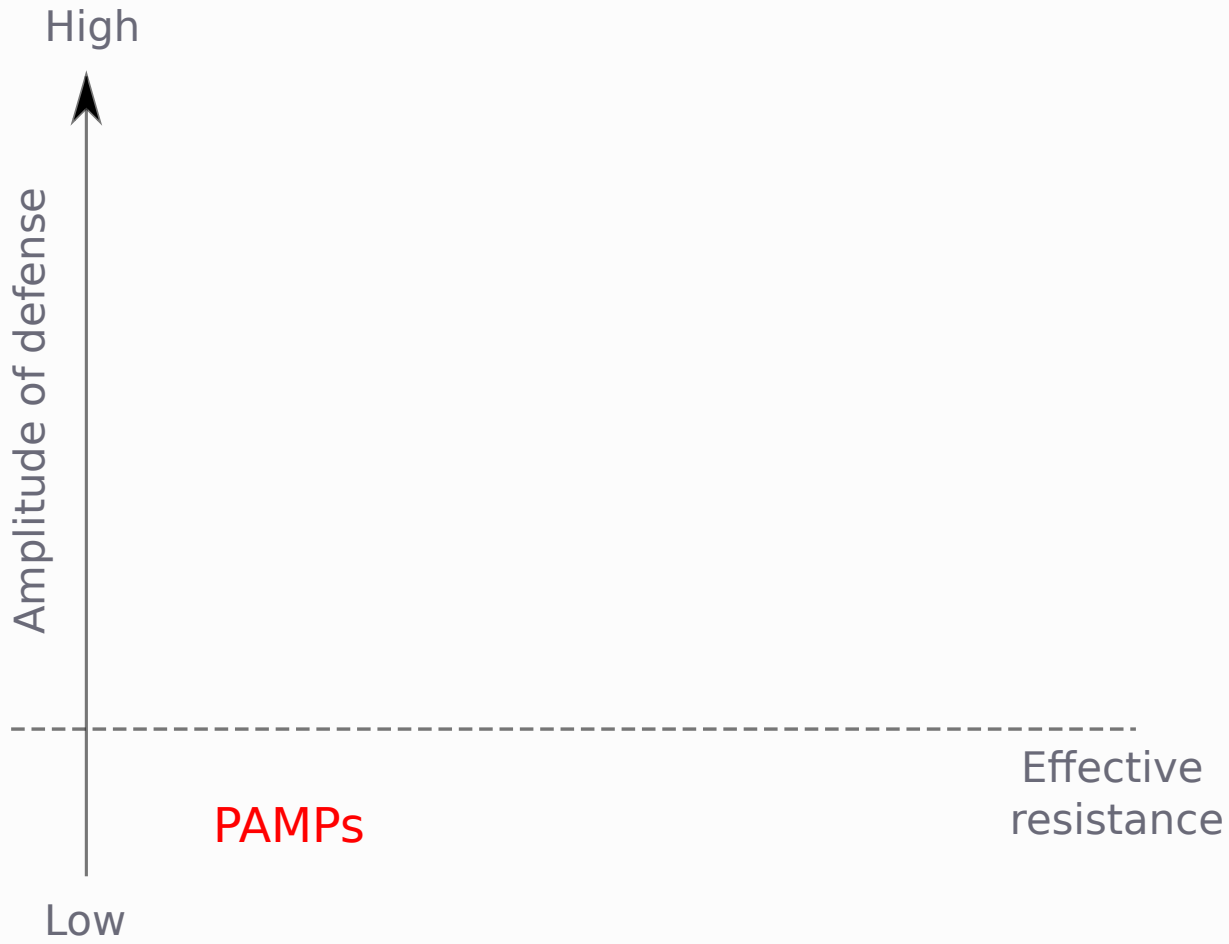
Only positive loops

$\Longrightarrow$

The system converges towards an equilibrium which can only be the coexistence equilibrium!

Plant immune system

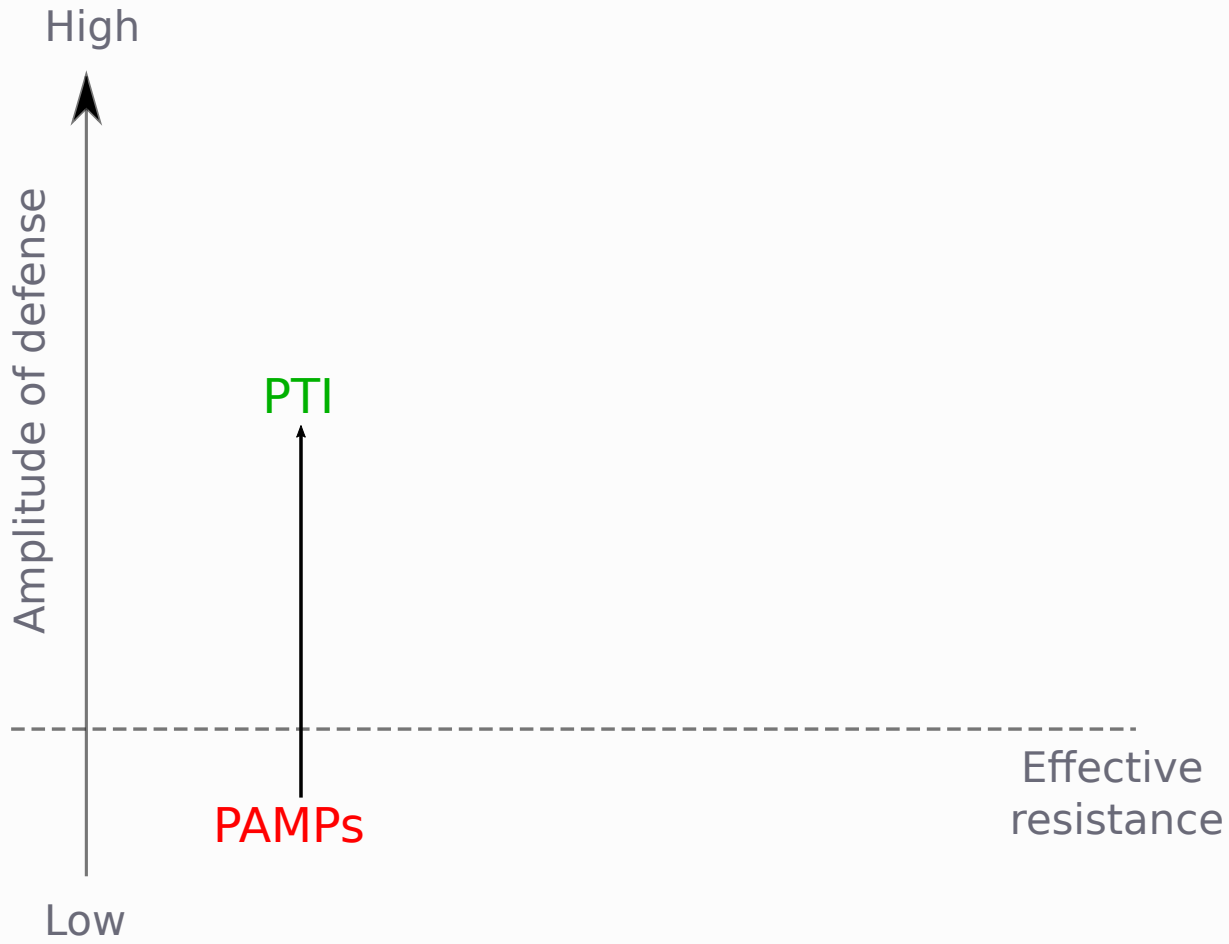
2 levels of immunity (Jones and Dangl, 2006; Milgroom, 2015)



PAMPs = Pathogen molecules, **PTI** = PAMP triggered immunity,
ETI = Effector triggered immunity

Plant immune system

2 levels of immunity (Jones and Dangl, 2006; Milgroom, 2015)



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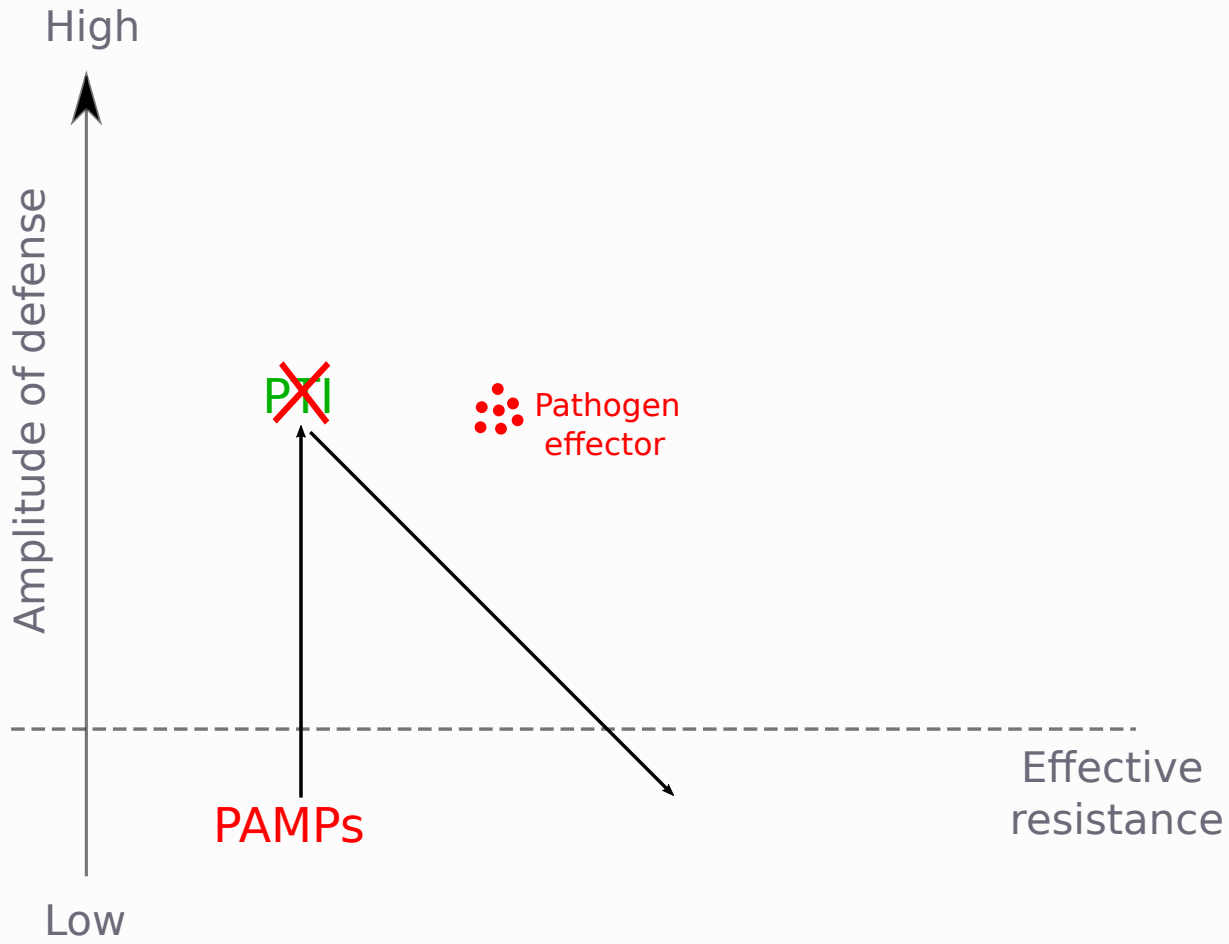

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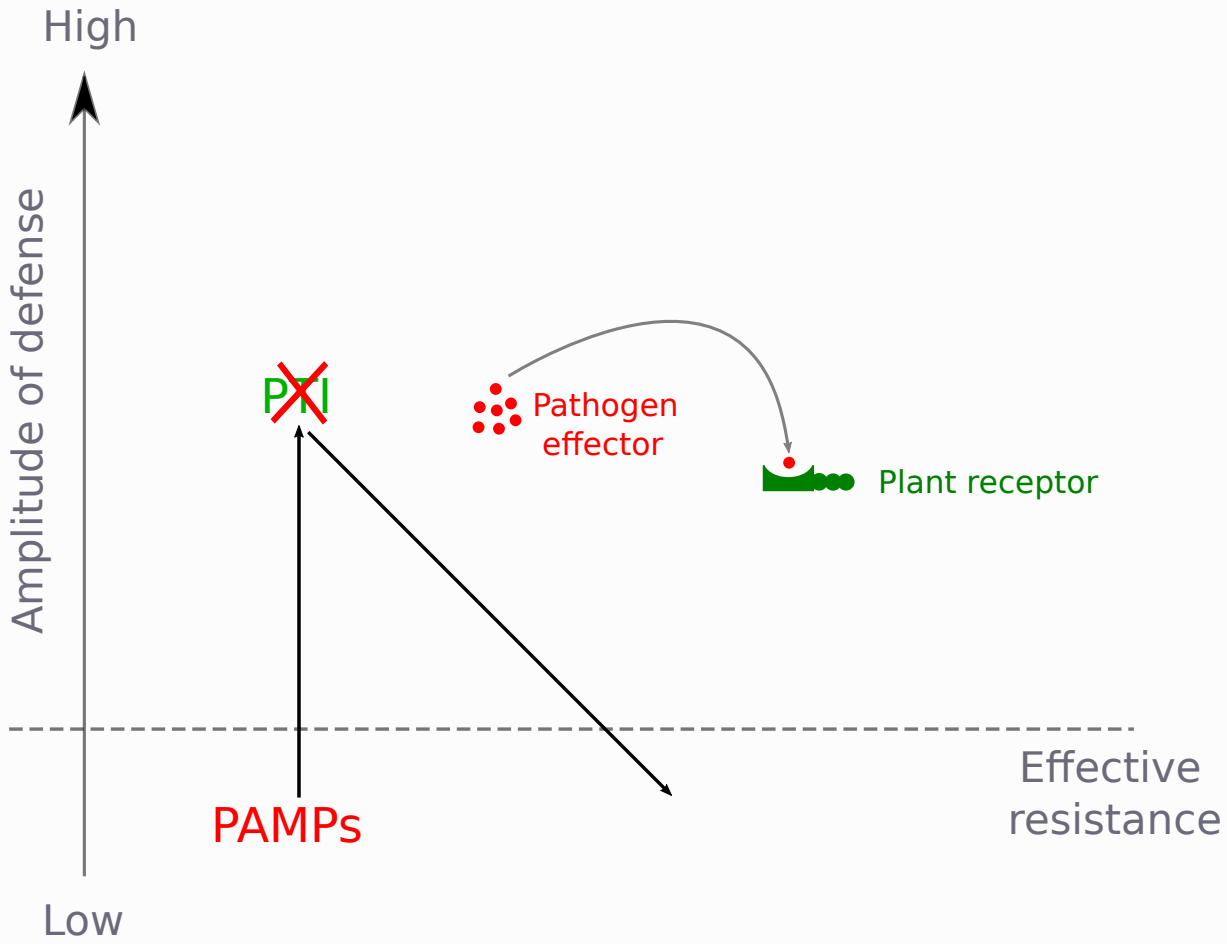

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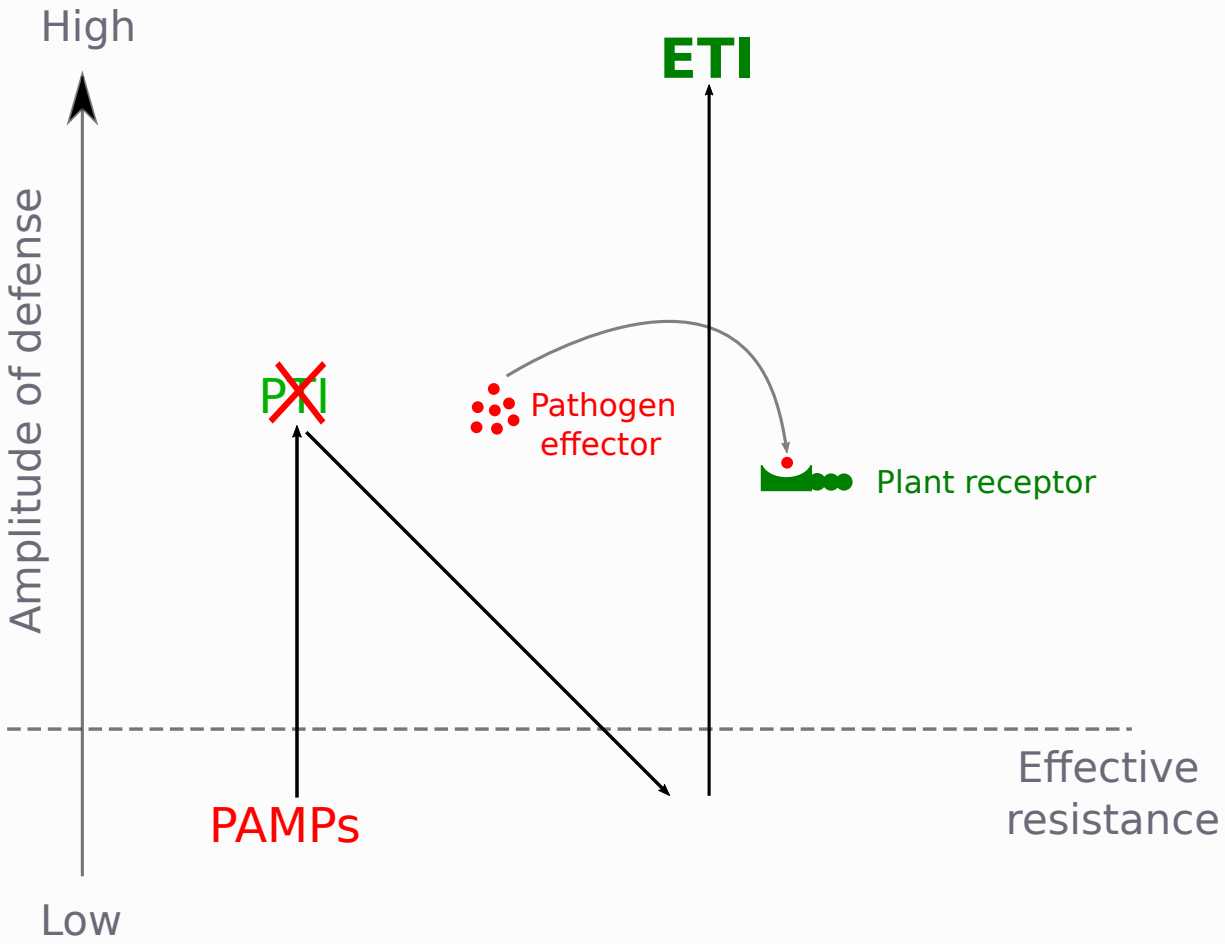

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