STERILITY IN TROUBLE: When Pest Mating Challenges Sterile Insect Technique

Marine Courtois

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INRAE Inria UNIVERSITÉ CÔTE D'AZUR cnrs Institut Sophia Agrobiotech SANTE DES PLANTES - ENVIRONNEMENT SMAI société de mathématiques appliquées et industrielles

Context

Sterile Insect Technique (SIT)

- Alternative technique to pesticides, **specific to the targeted pest (autocide)**
- Technique emerged in the **1930s-1950s** (Dyck et al. 2021)
- Concept: **release sterile males** into the wild **to disrupt the insects' reproductive cycle** (↘ the number of offspring)

📷 *U.S. Department of Agriculture*

Edward F. Knipling
American entomologist

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First major success

Screw-worm fly
Cochliomyia hominivorax

➤ heavy losses in the livestock sector

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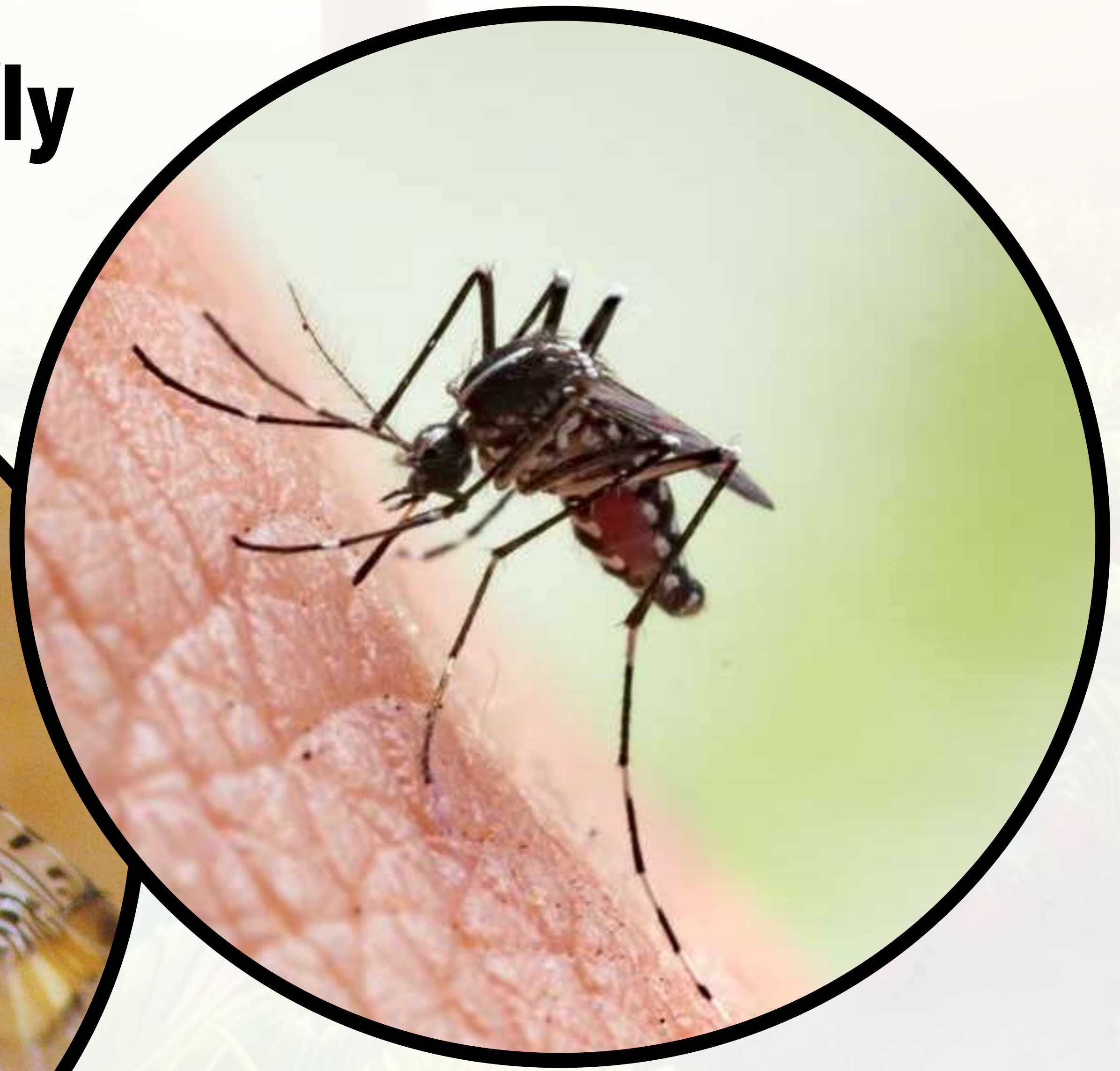
➤ heavy losses in the livestock sector

Mediterranean fruit fly
Ceratitis capitata

➤ dreaded in world agriculture



Tiger mosquito
Aedes albopictus

➤ disease vector (dengue fever, malaria, Zika)

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Mass-rearing of targeted insects

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Separation to keep only males

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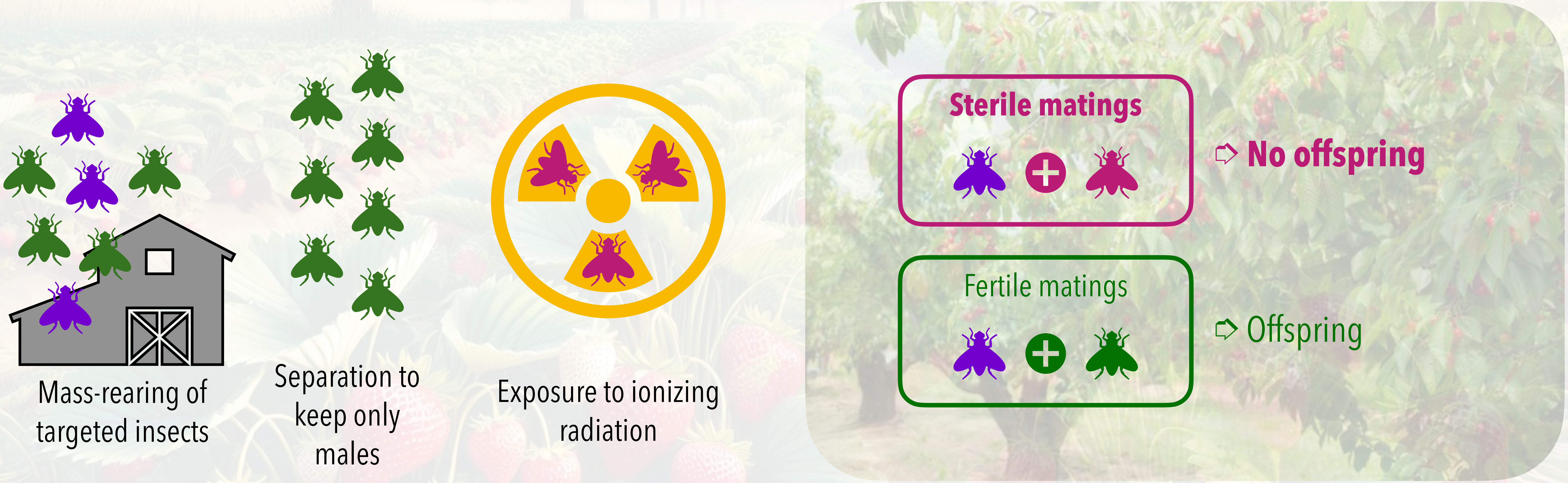

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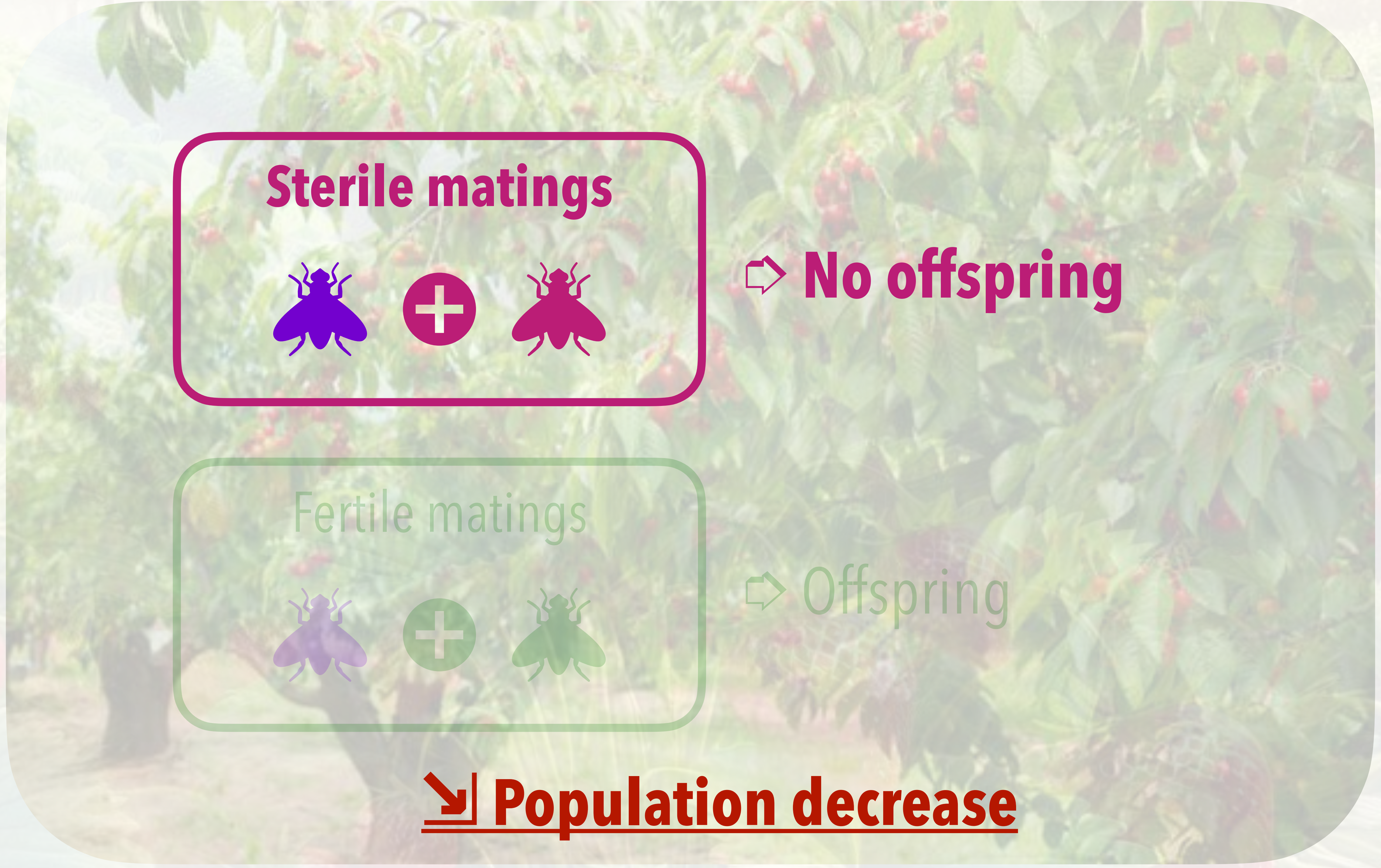

Challenges - Scientific question

Several factors can interfere with SIT effectiveness:

PRODUCTION | **SEXING** | **STERILIZATION** | **MASS RELEASES** | **DILUTION OF WILD POPULATIONS**

Mass-rearing of targeted insects

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Sterile matings ➪ **No offspring**

Fertile matings ➪ Offspring

↘ Population decrease

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- **Residual fertility (RF):** imperfect sterilization

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↗ the number of **males available** in the environment **to produce offspring**

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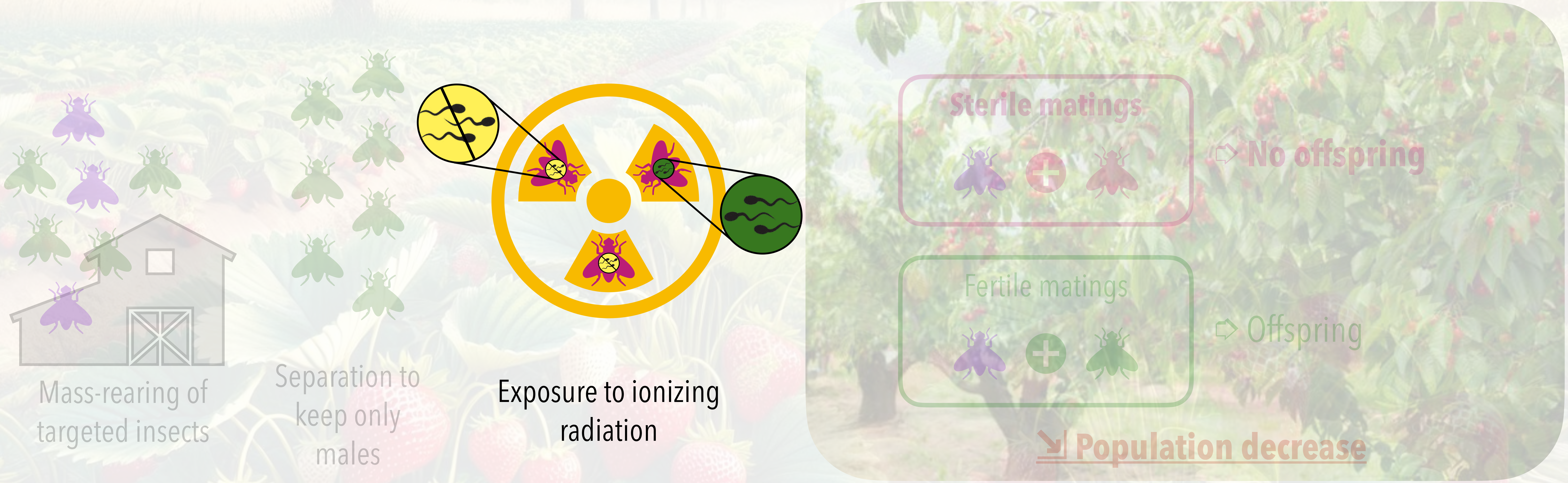

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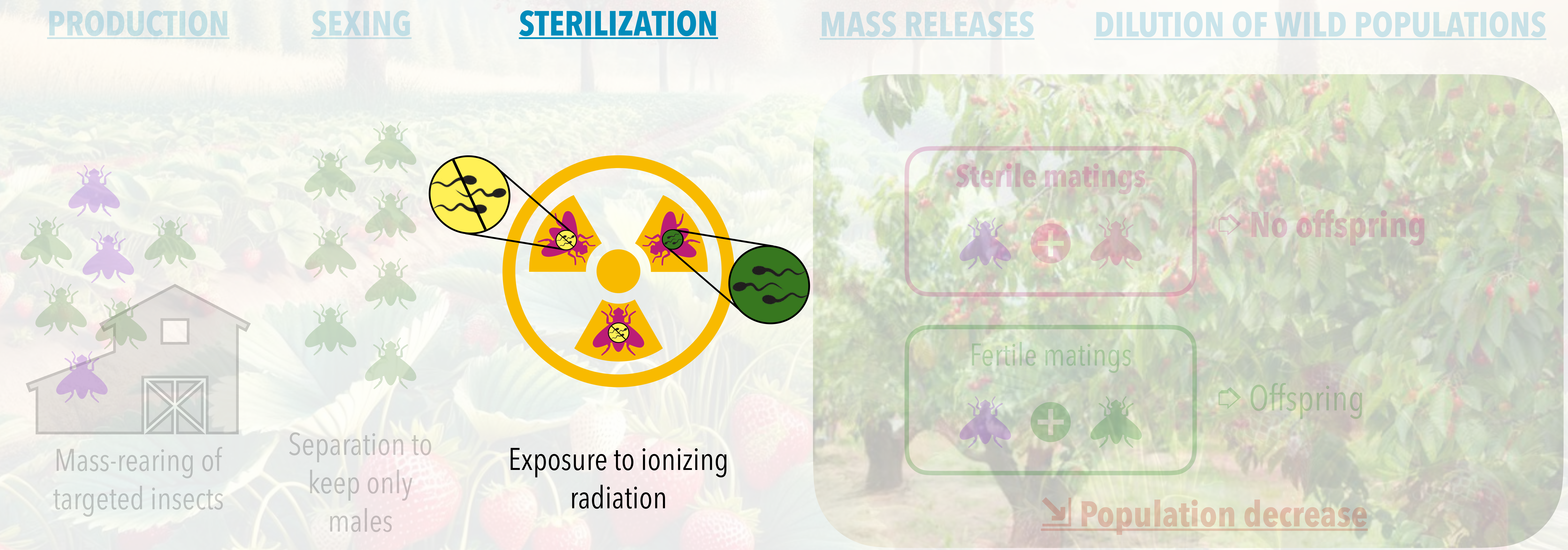

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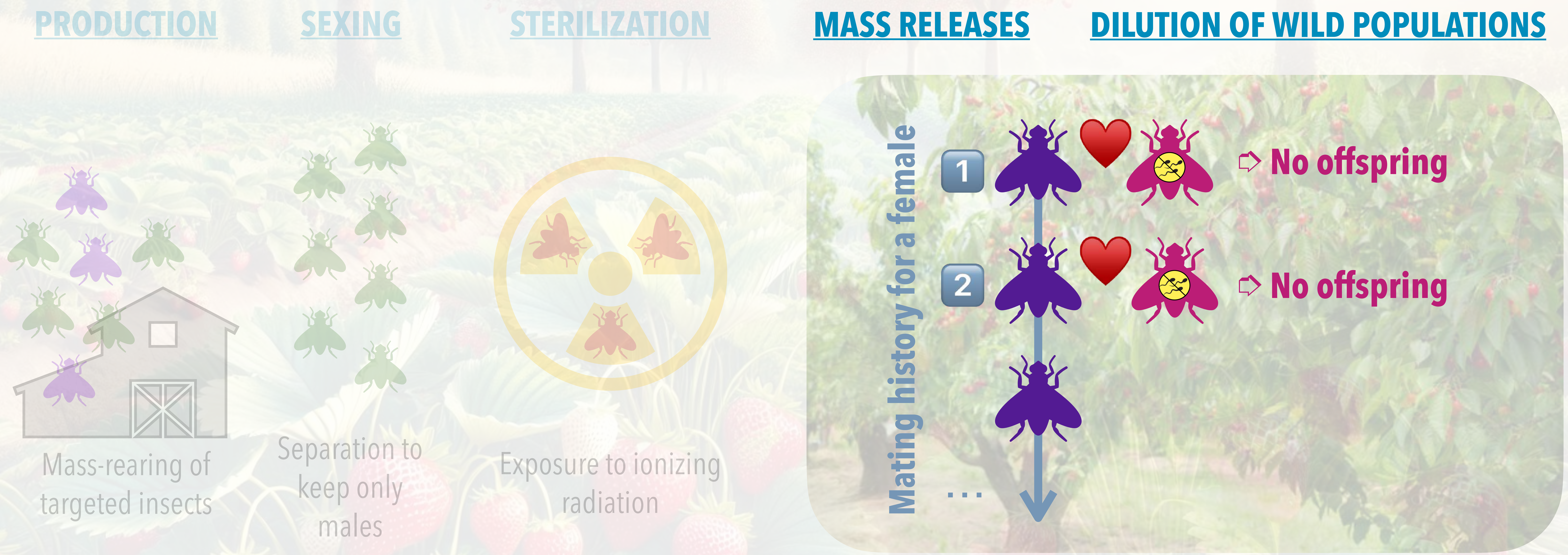

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PRODUCTION SEXING STERILIZATION MASS RELEASES DILUTION OF WILD POPULATIONS

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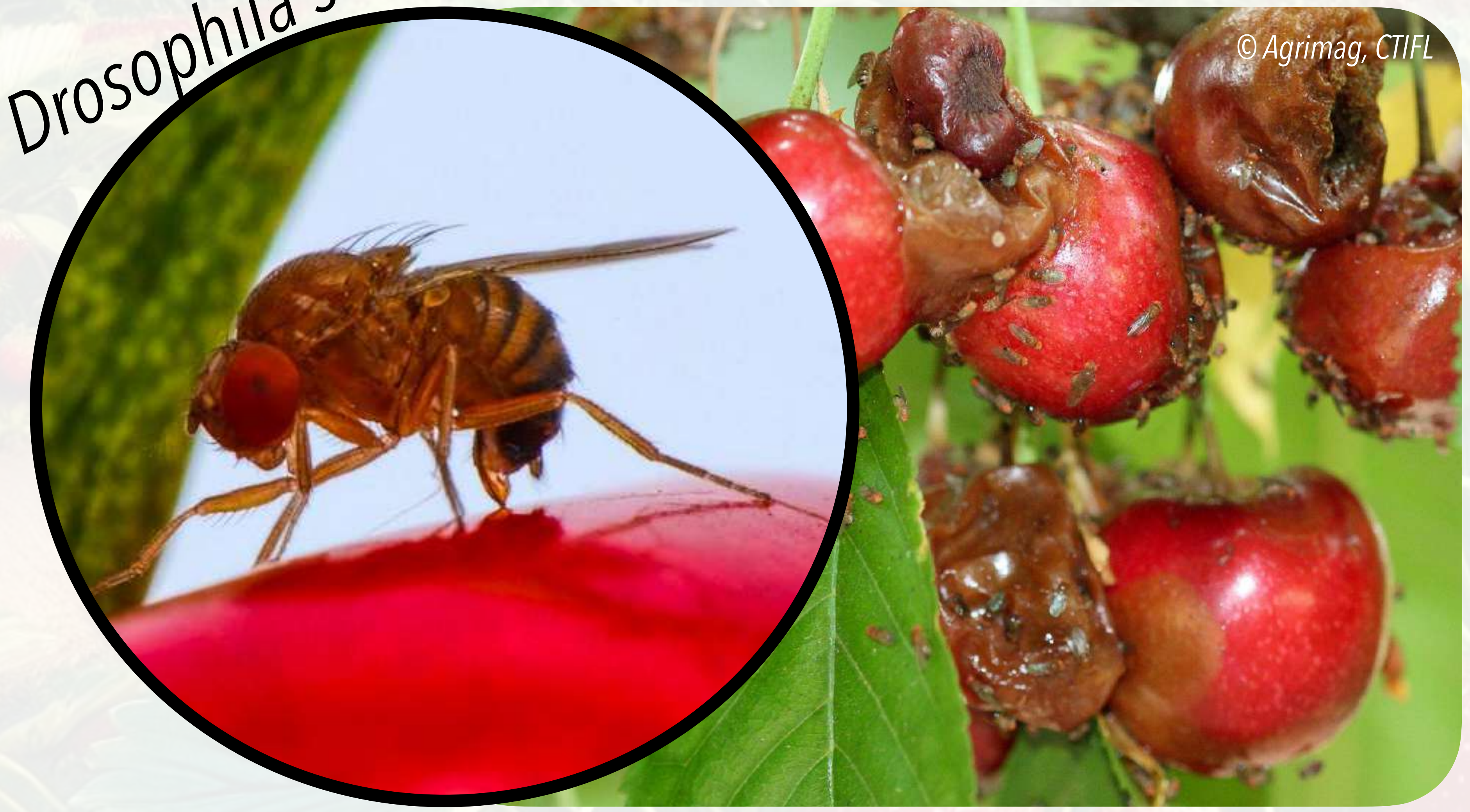
Ceratitis capitata

CeraTIS-Corse (projet Ecophyto 2020-2023)

Drosophila suzukii

SuzuKIISS:me (ANR maturation 2022-2025)



Losses up to **100% of the production** (Jerraya 2003; Ryckewaert et al. 2010, Mazzi et al. 2017)

Highly **polyphagous** (Green et al. 2019)

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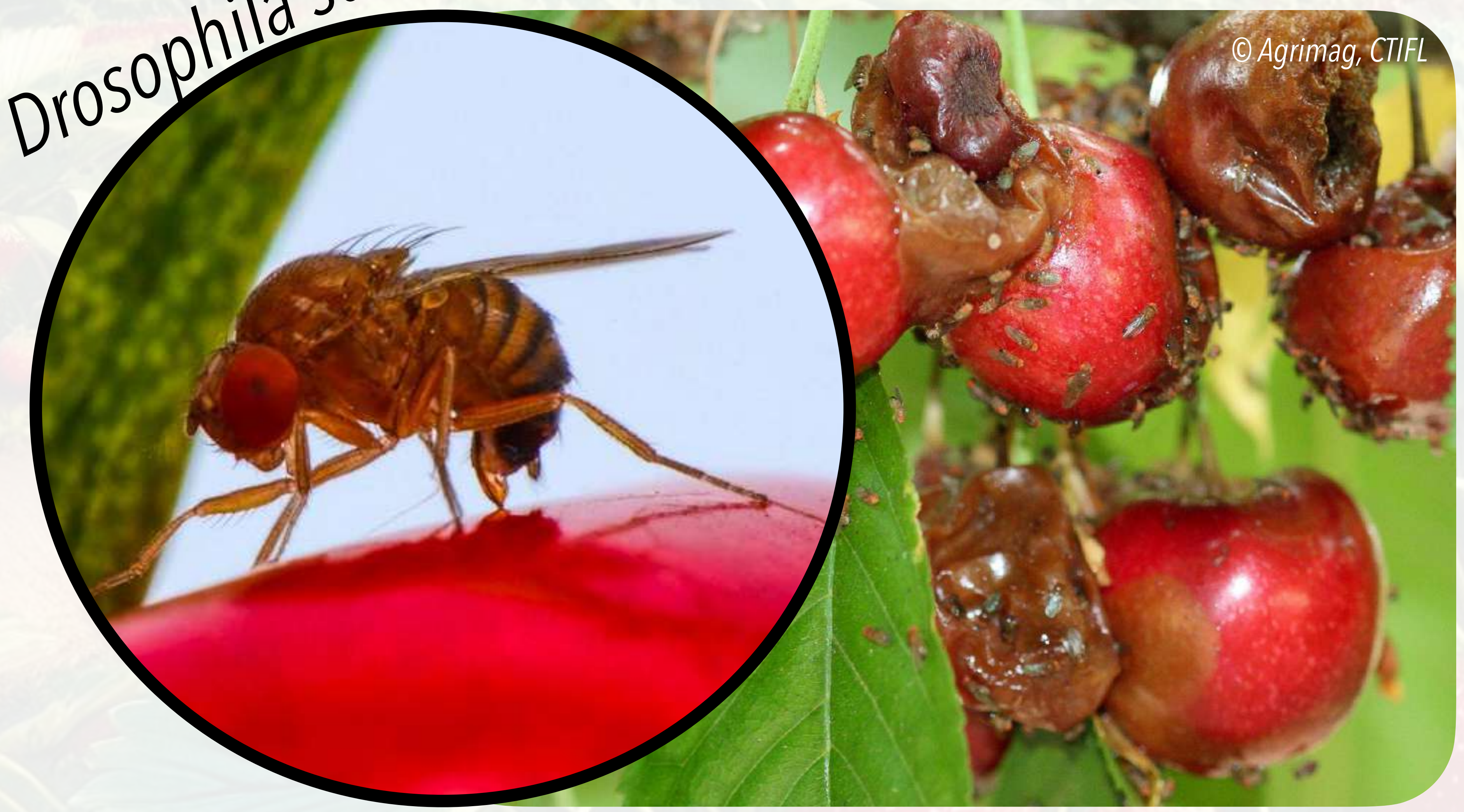

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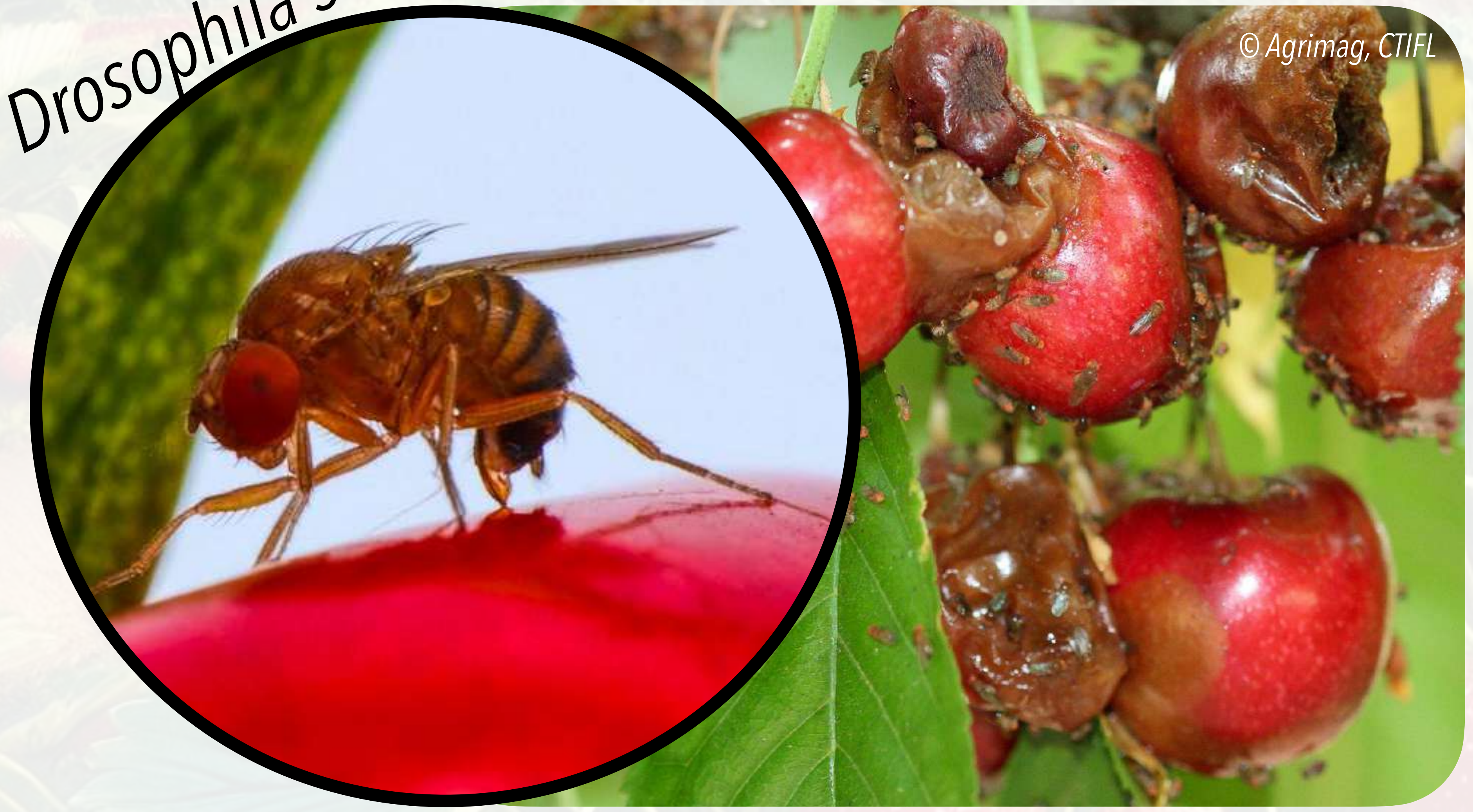
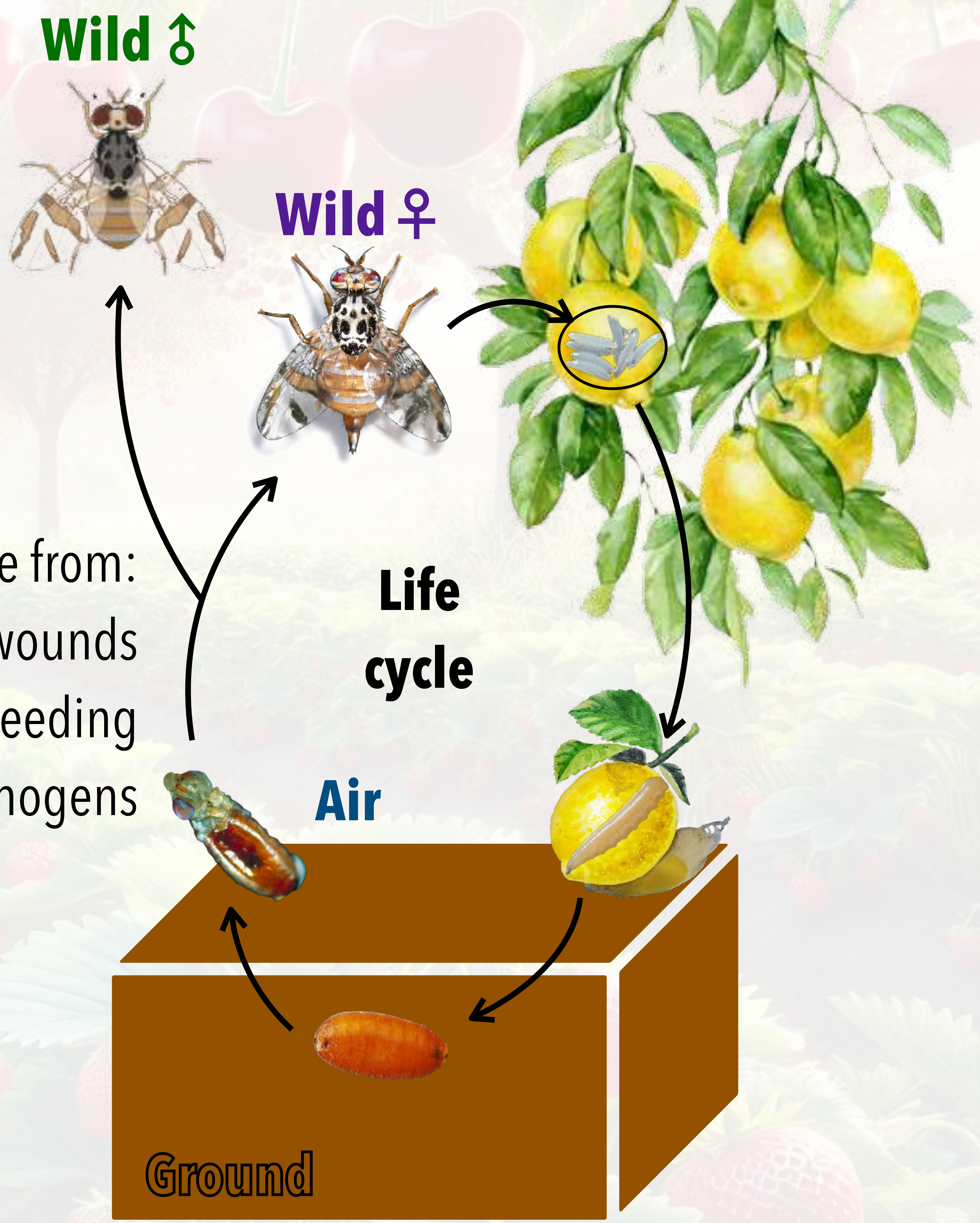


Highly **polyphagous** (Green et al. 2019)

Damage arise from:
oviposition wounds
internal larval feeding
pathogens



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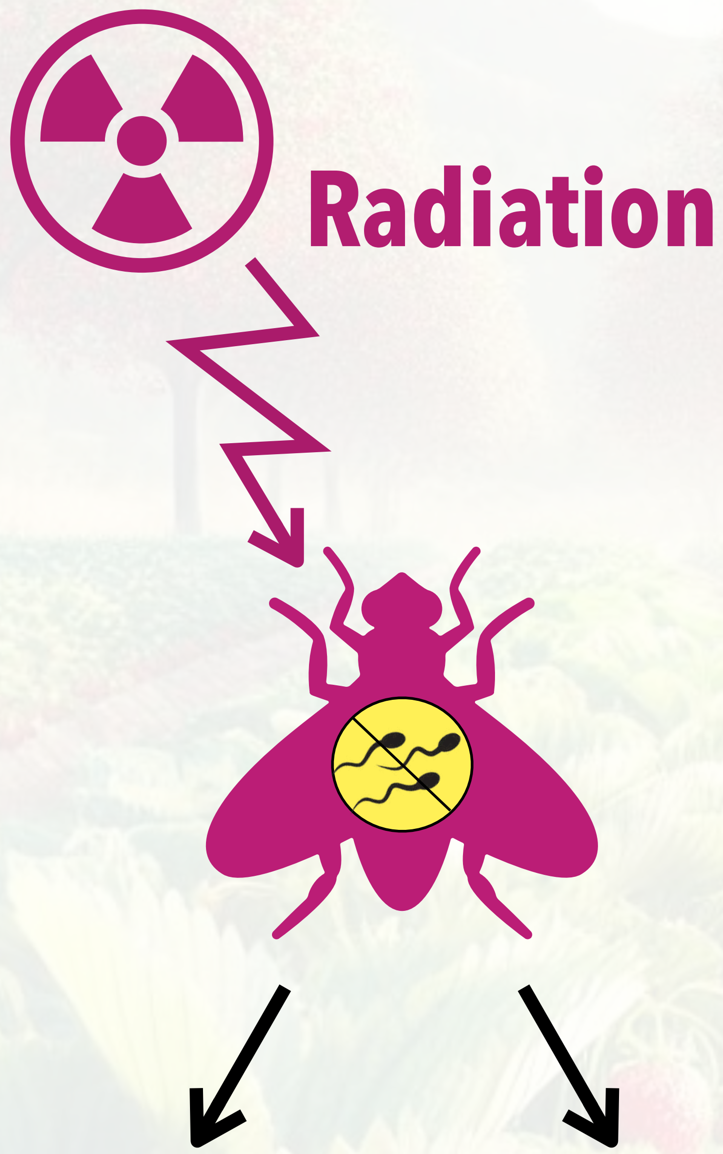
(1) **Residual fertility**: imperfect sterilization

How low residual fertility rate should be to ensure pest control?

- **An irradiation dose inducing 100% sterility** is rarely used in SIT programs (Robinson. 2005, Bakri and Mehta. 2005)



If high doses: loss of attractiveness
(Bakri et al, 2005)

Sterility **Competitiveness**

➡️ Trade-off
(Parker et Mehta, 2007)

(1) **Residual fertility**: imperfect sterilization

How low residual fertility rate should be to ensure pest control?

Sterilized males

S

Wild females

F

M

Wild males

$$\begin{cases} \dot{M} = -\mu_M M + rp\dfrac{M+\epsilon\eta S}{k+M+\eta S}C(F)F + \delta\sigma \\[2ex] \dot{F} = -\mu_F F + r(1-p)\dfrac{M+\epsilon\eta S}{k+M+\eta S}C(F)F \\[2ex] \dot{S} = -\mu_S S + (1-\delta)\sigma \end{cases}$$

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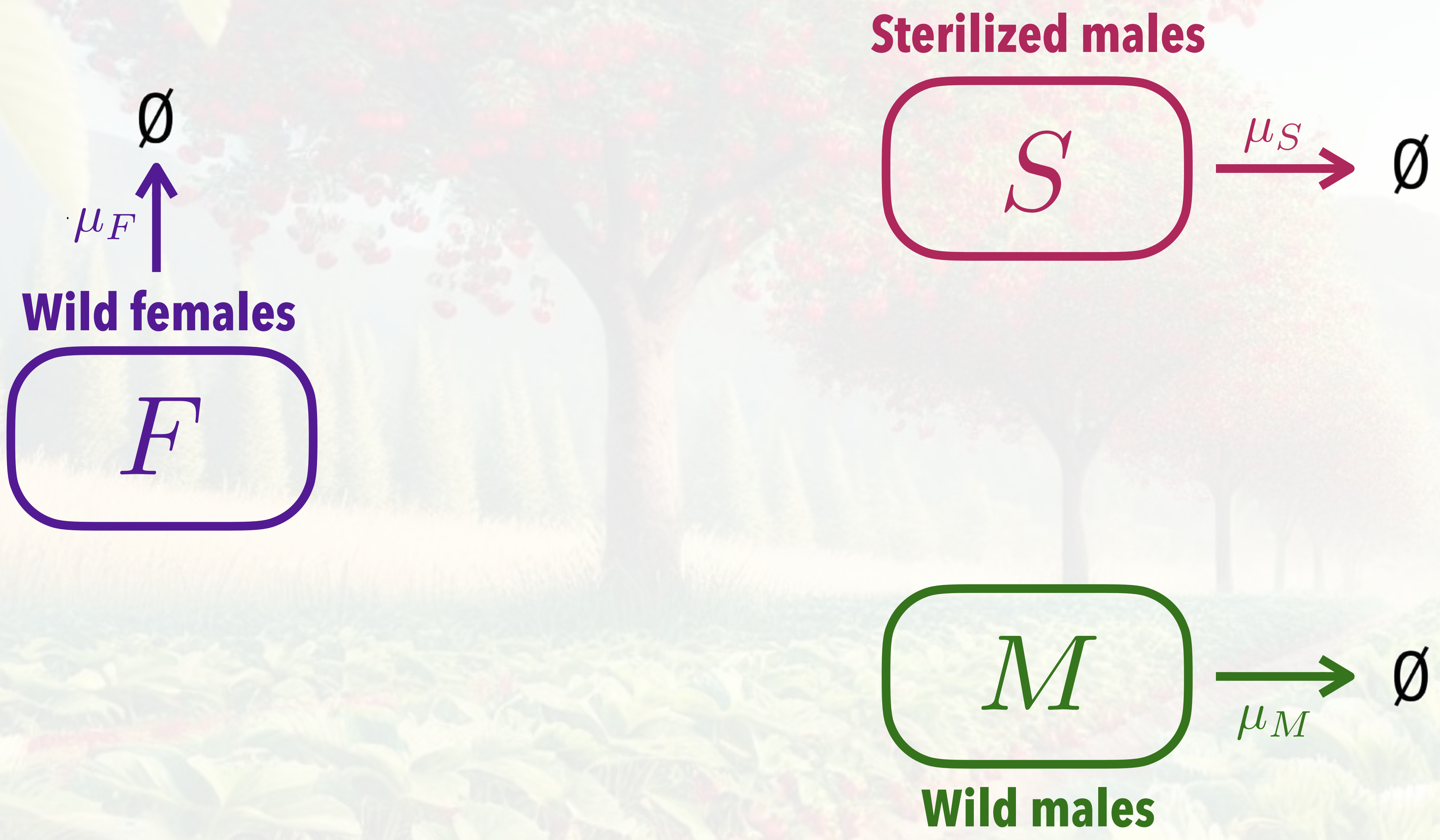

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μ_x Mortality rate

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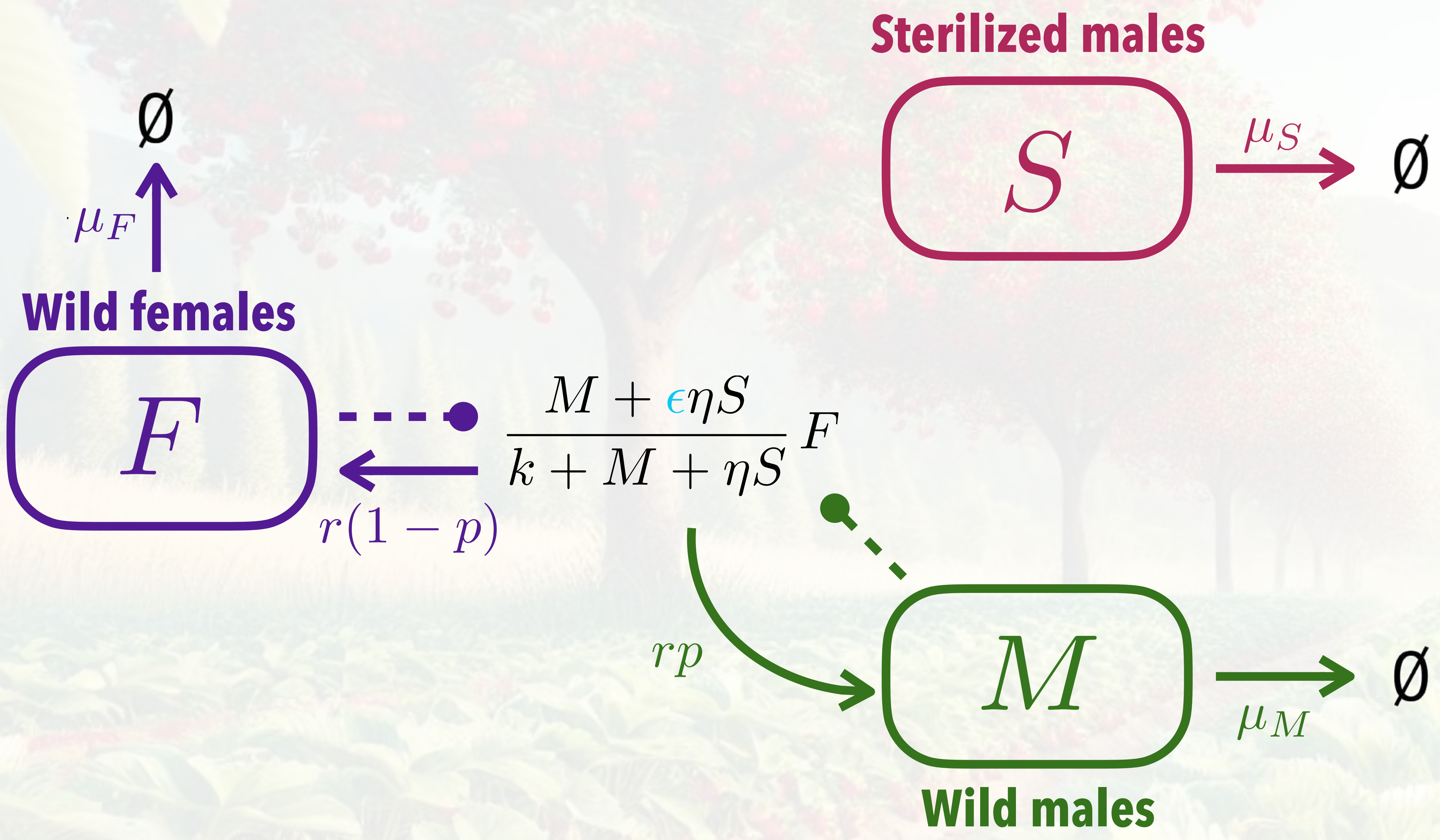

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μ_x	Mortality rate
p	Sex ratio
r	Emergence rate
k	Mating half-saturation constant
$1-\eta$	Sterilization cost
σ	Sterilized male release rate

$$C(F) = \frac{1}{1+\beta F}$$

Residual fertility study:

- No ~~residual fertility~~ ($\boldsymbol{\delta} = 0$, $\epsilon = 0$)

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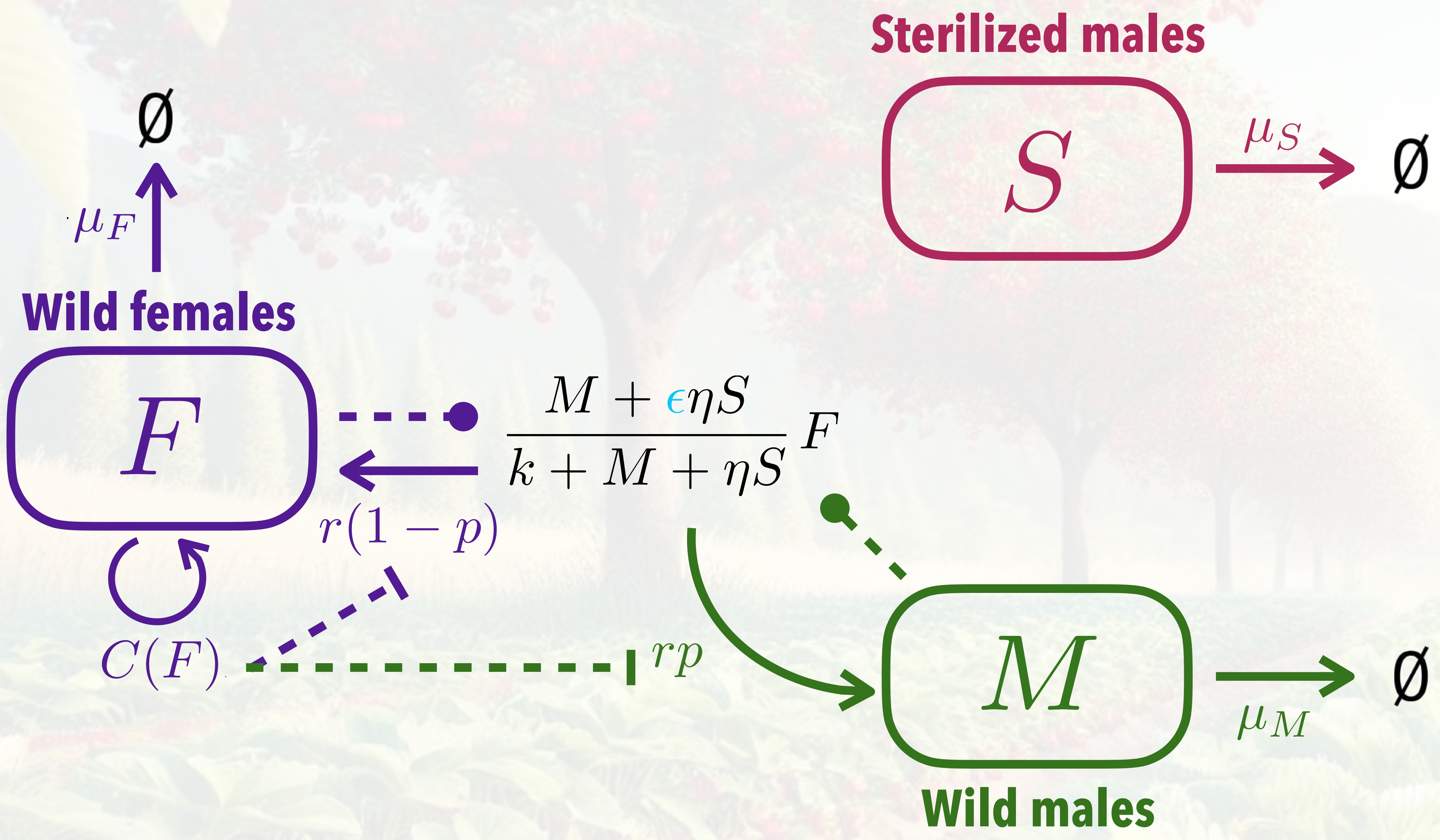

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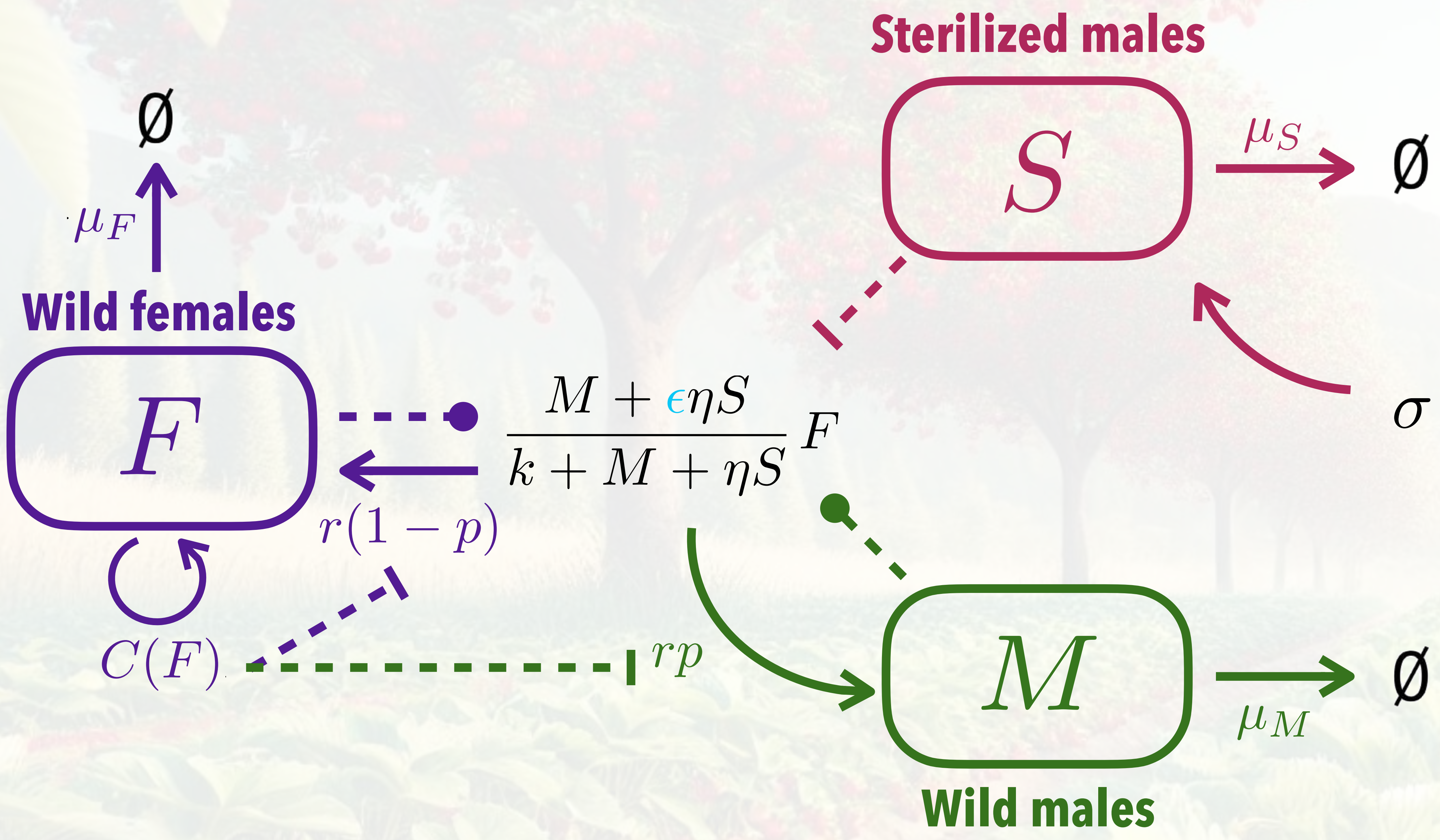

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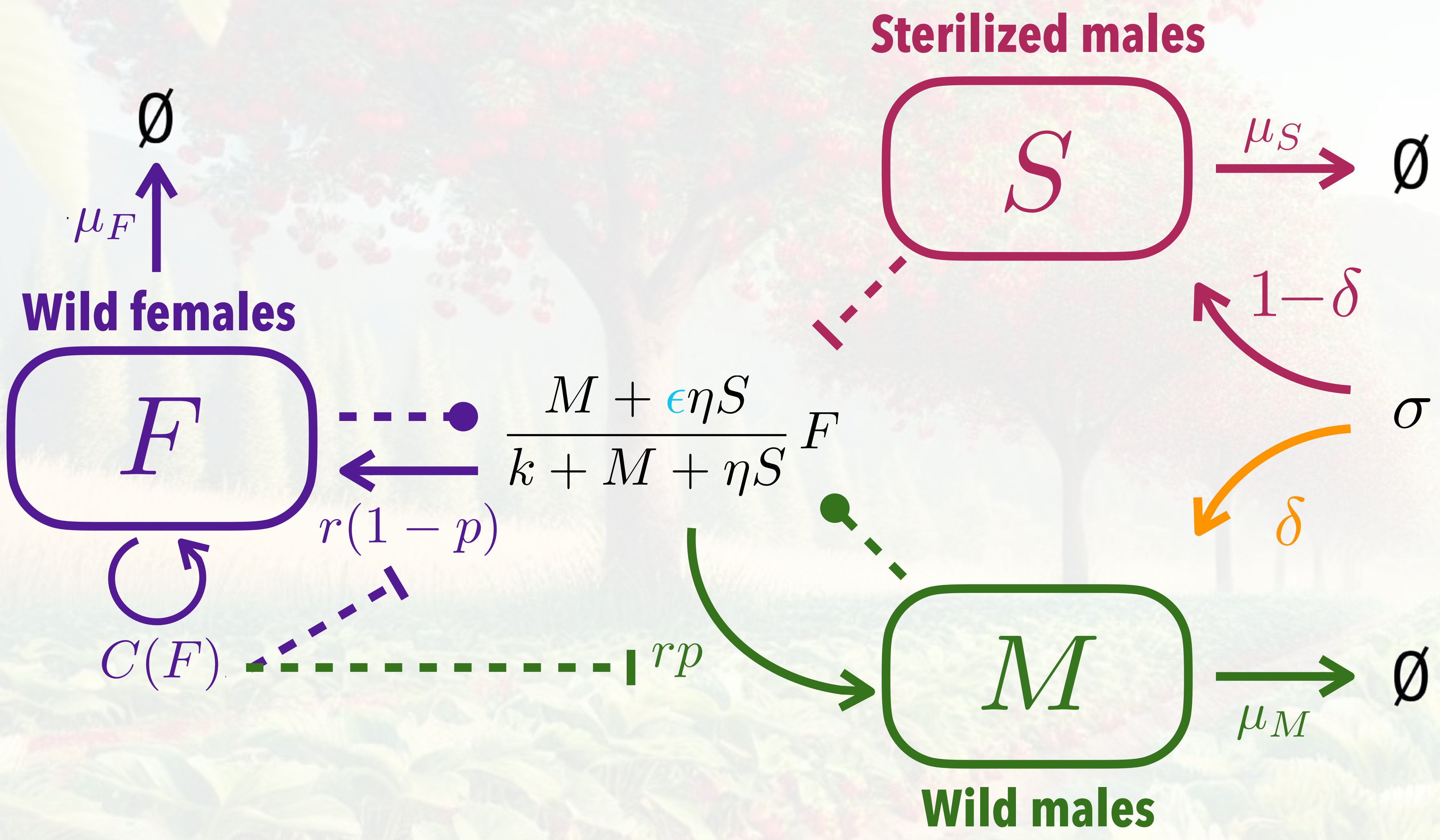

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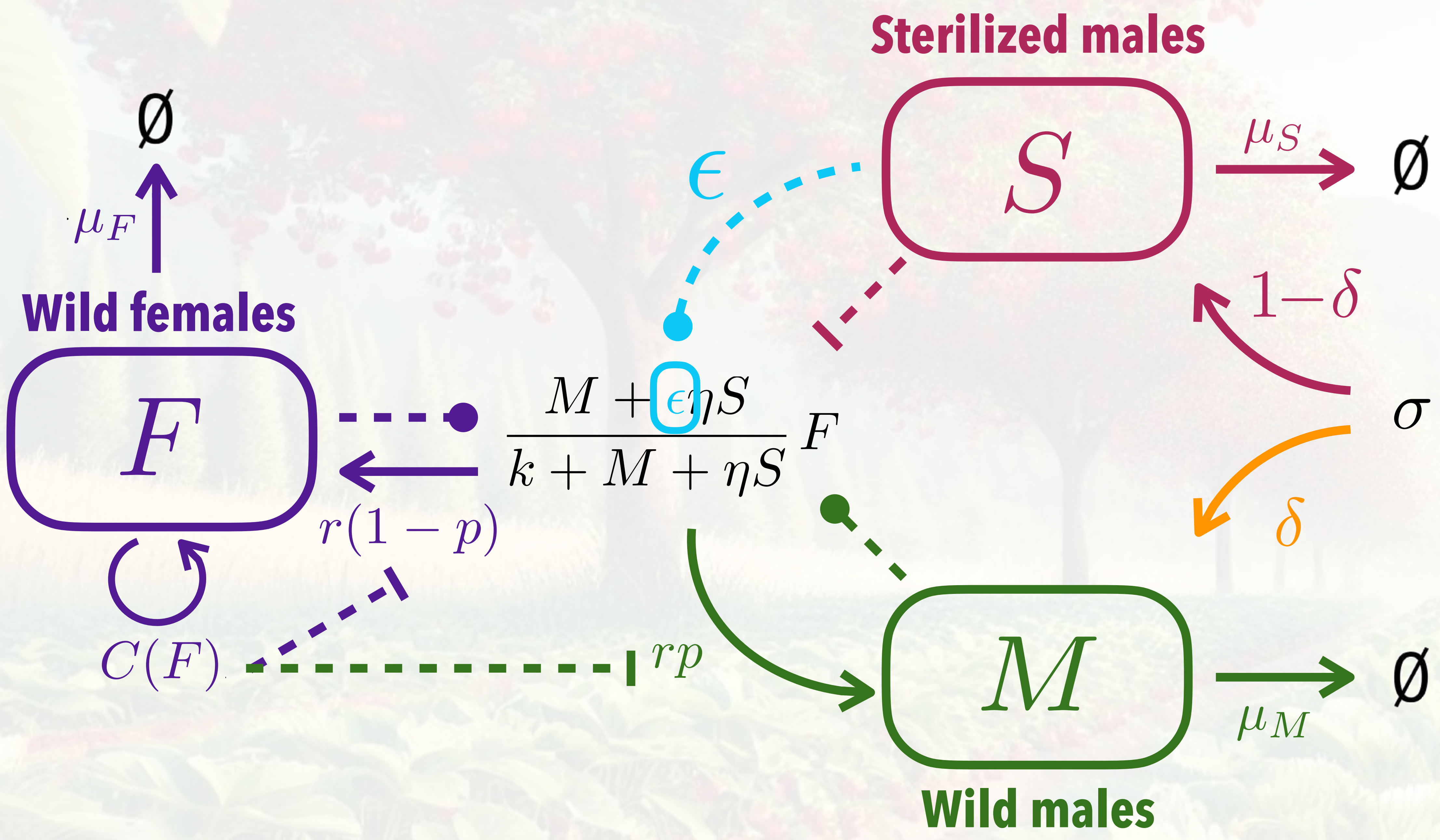

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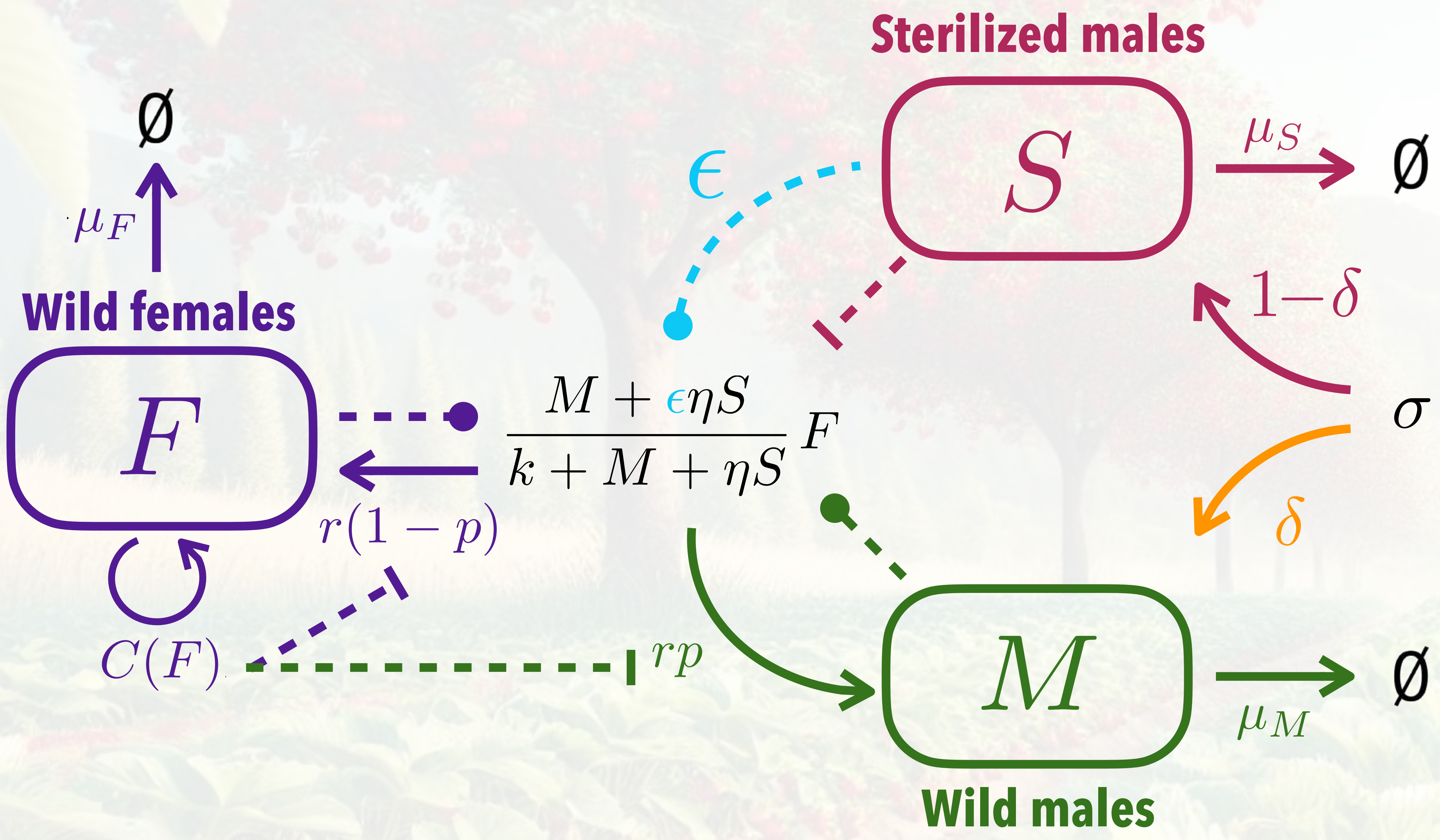

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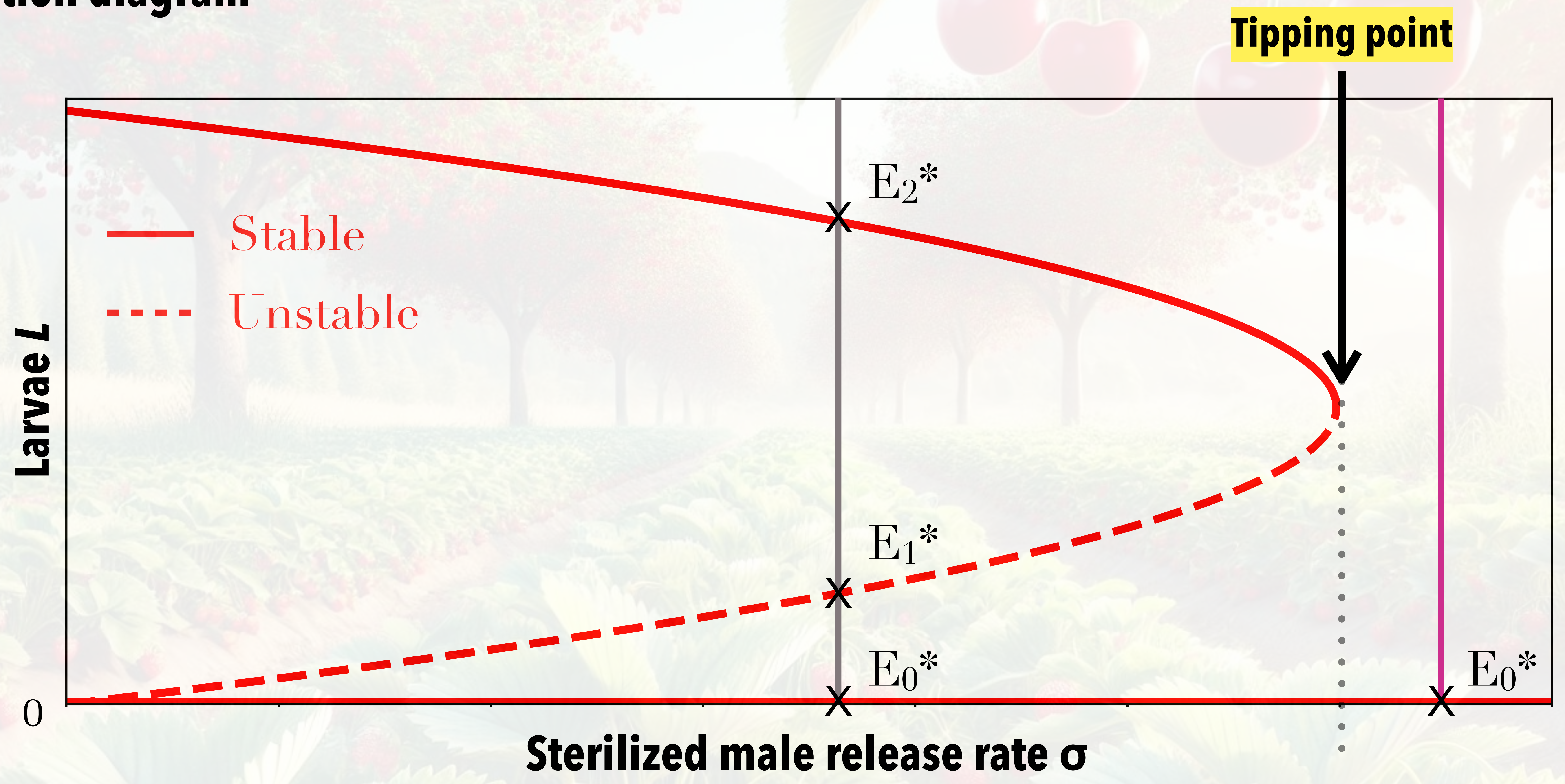
⇨ Equilibrium research

⇨ Stability study

⇨ Identification of situations where population densities can be controlled.

(1) **Residual fertility**: imperfect sterilization **How low residual fertility rate should be to ensure pest control?**

- **Bifurcation diagram**



- **When σ > tipping point:** pest-free equilibrium E_0* is LAS
- **When σ < tipping point:** convergence towards E_0* or E_2*

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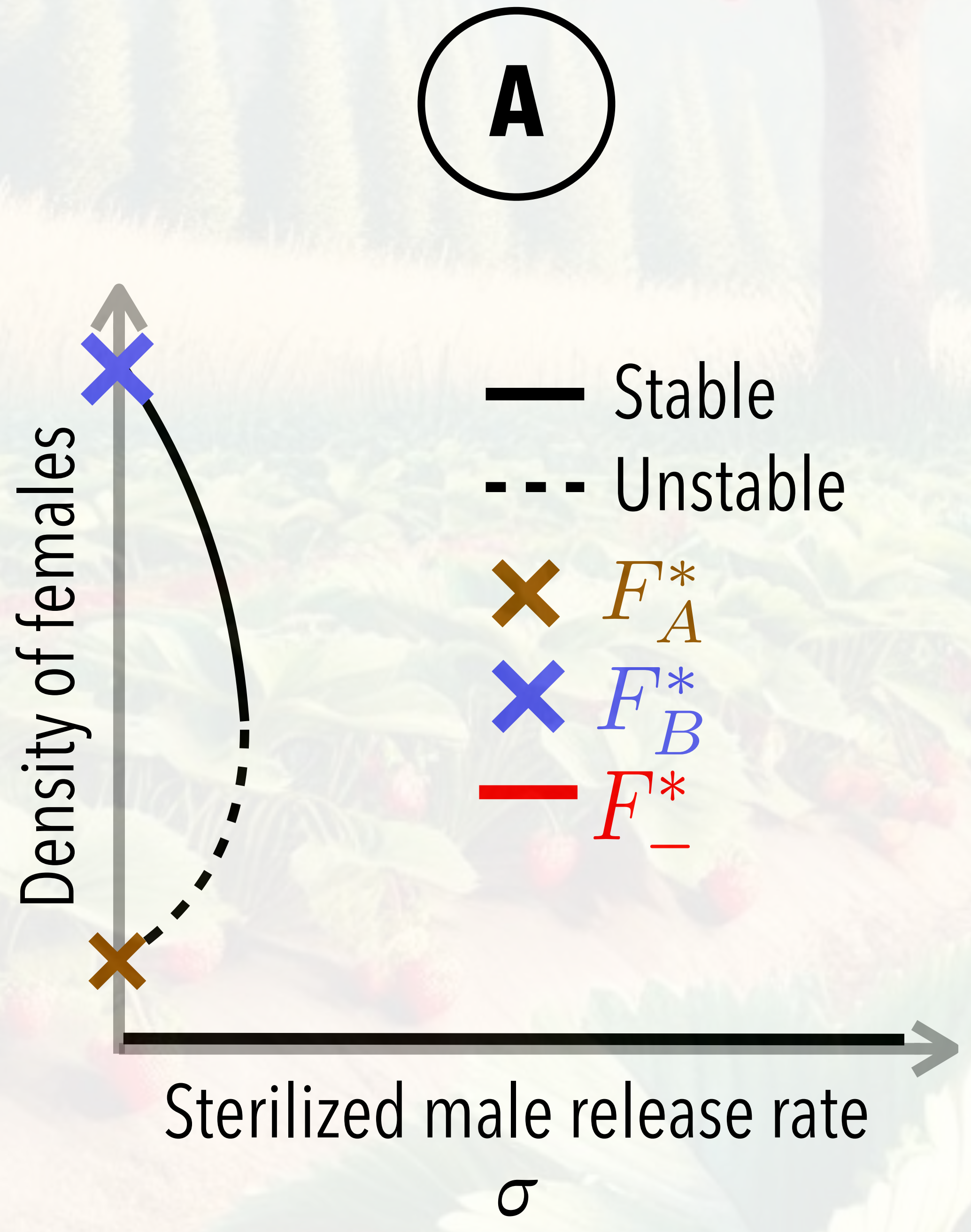
- **Bifurcation diagram**

Residual fertility rate



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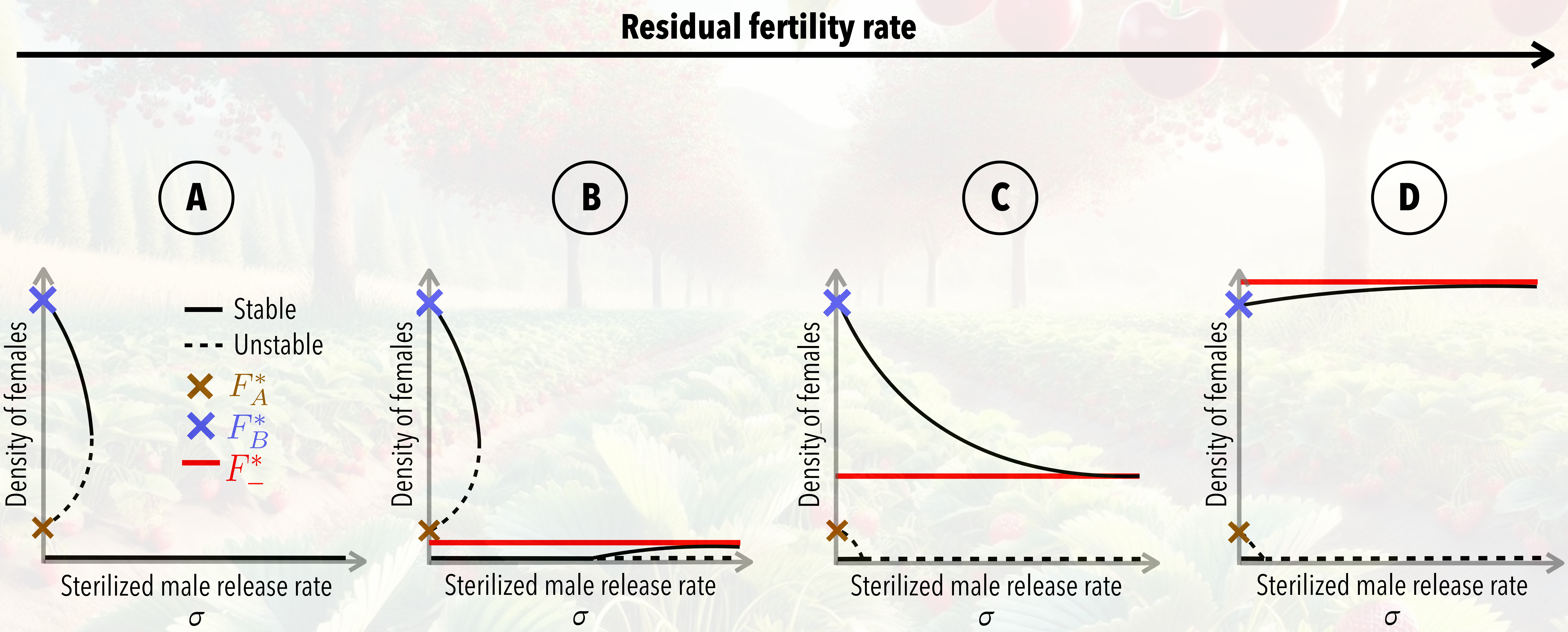

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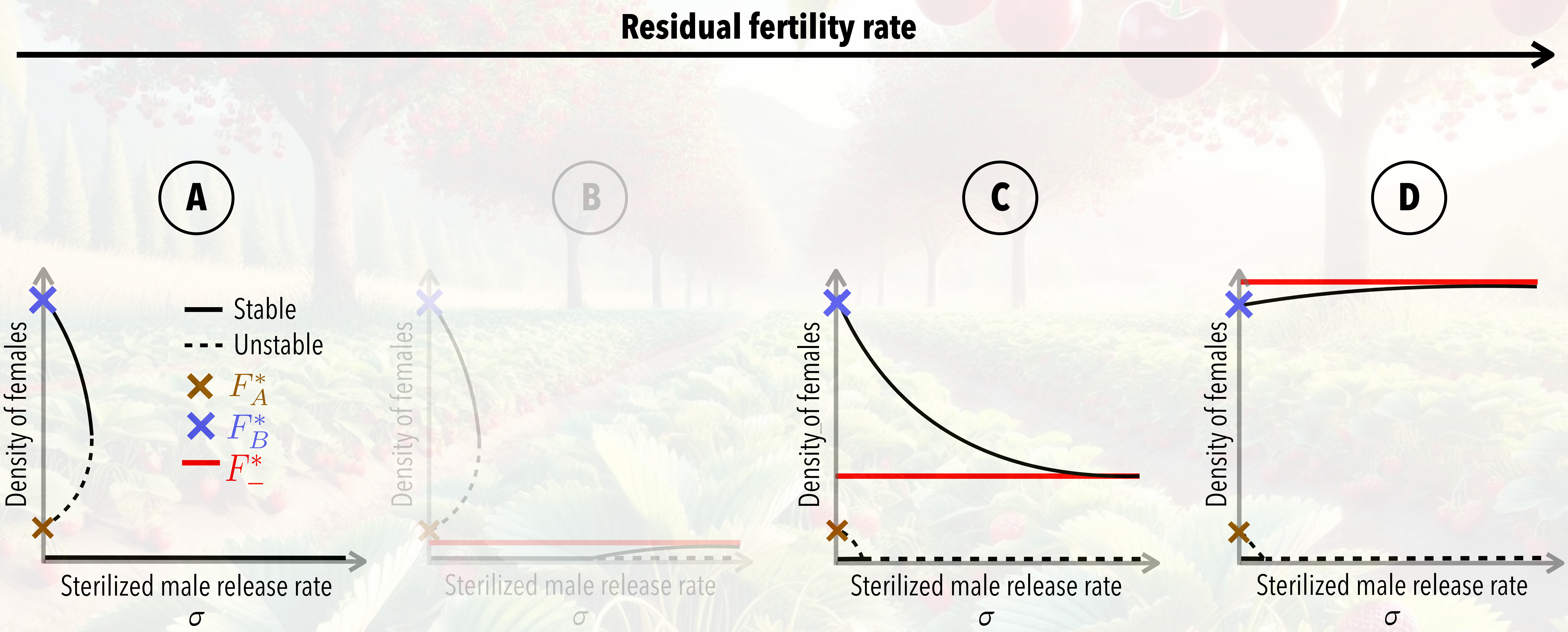

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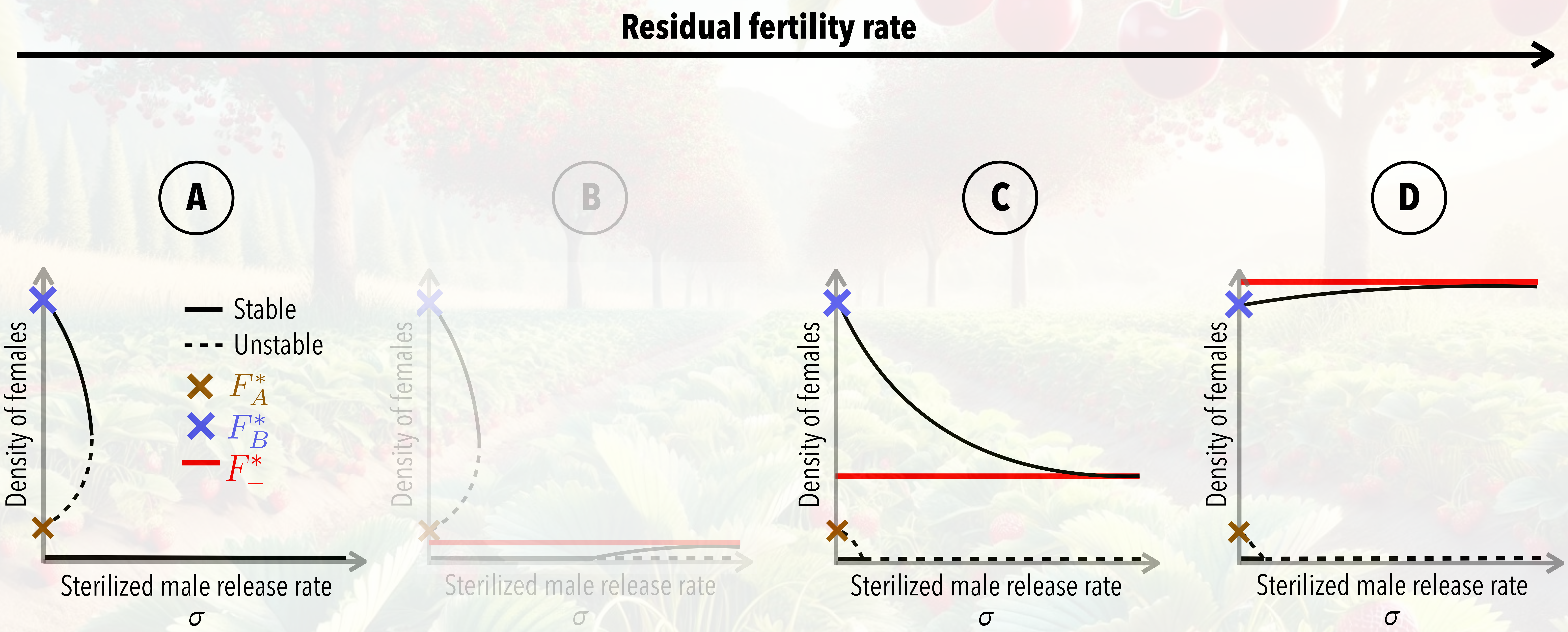

Eradication

Eradication
Quasi eradication

Control for large σ

SIT is inefficient

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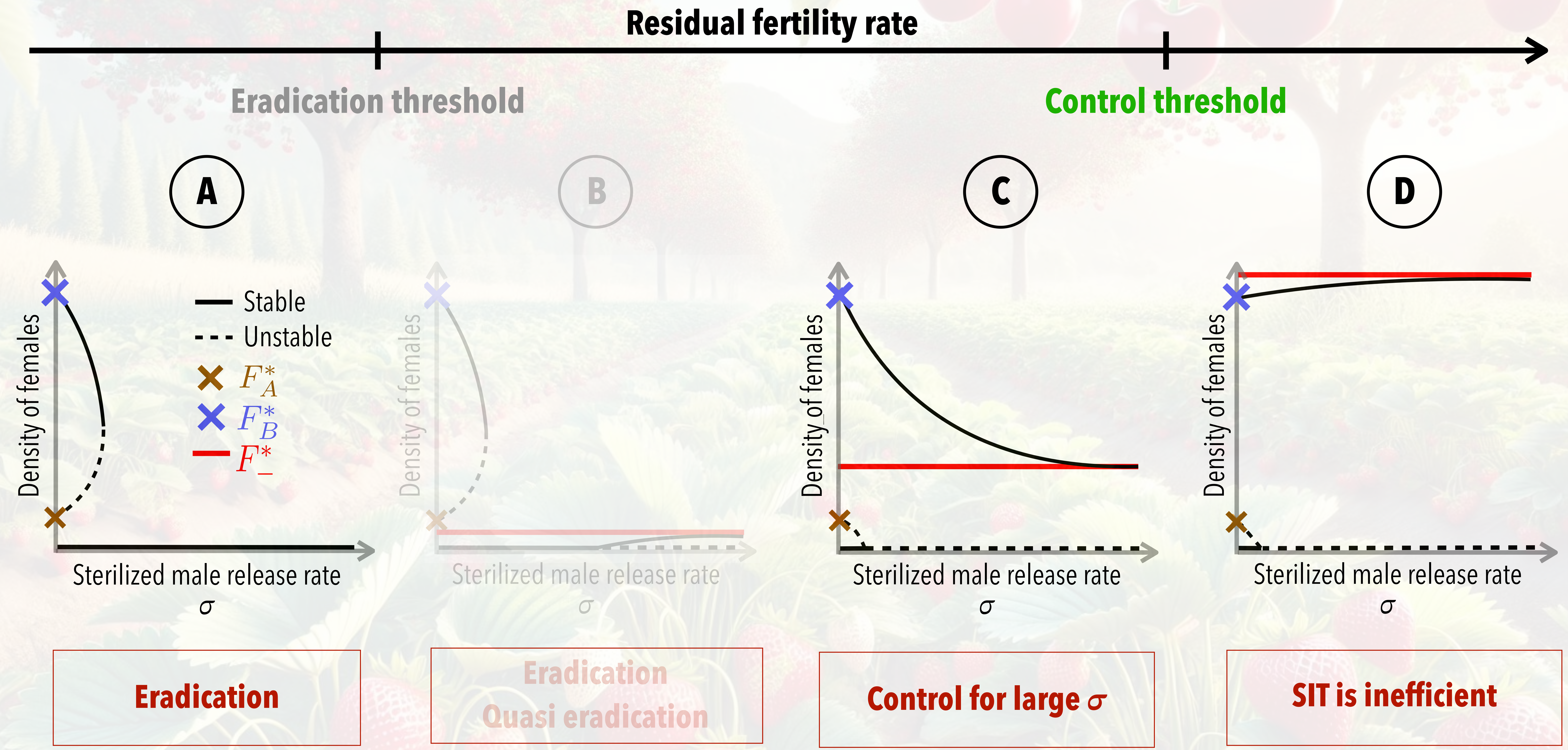
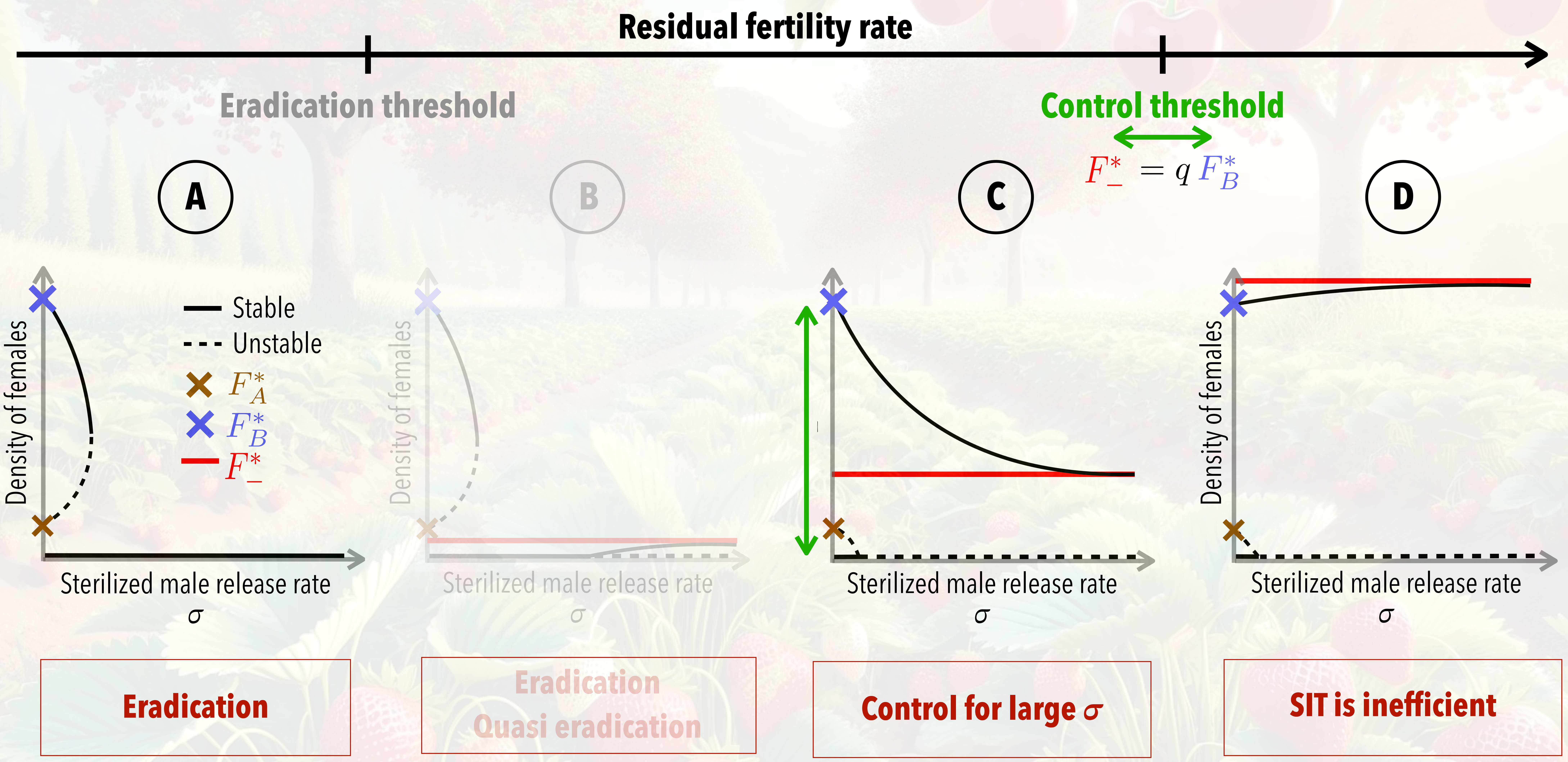
- **Bifurcation diagram**



(1) **Residual fertility**: imperfect sterilization

How low residual fertility rate should be to ensure pest control?

- **Bifurcation diagram**



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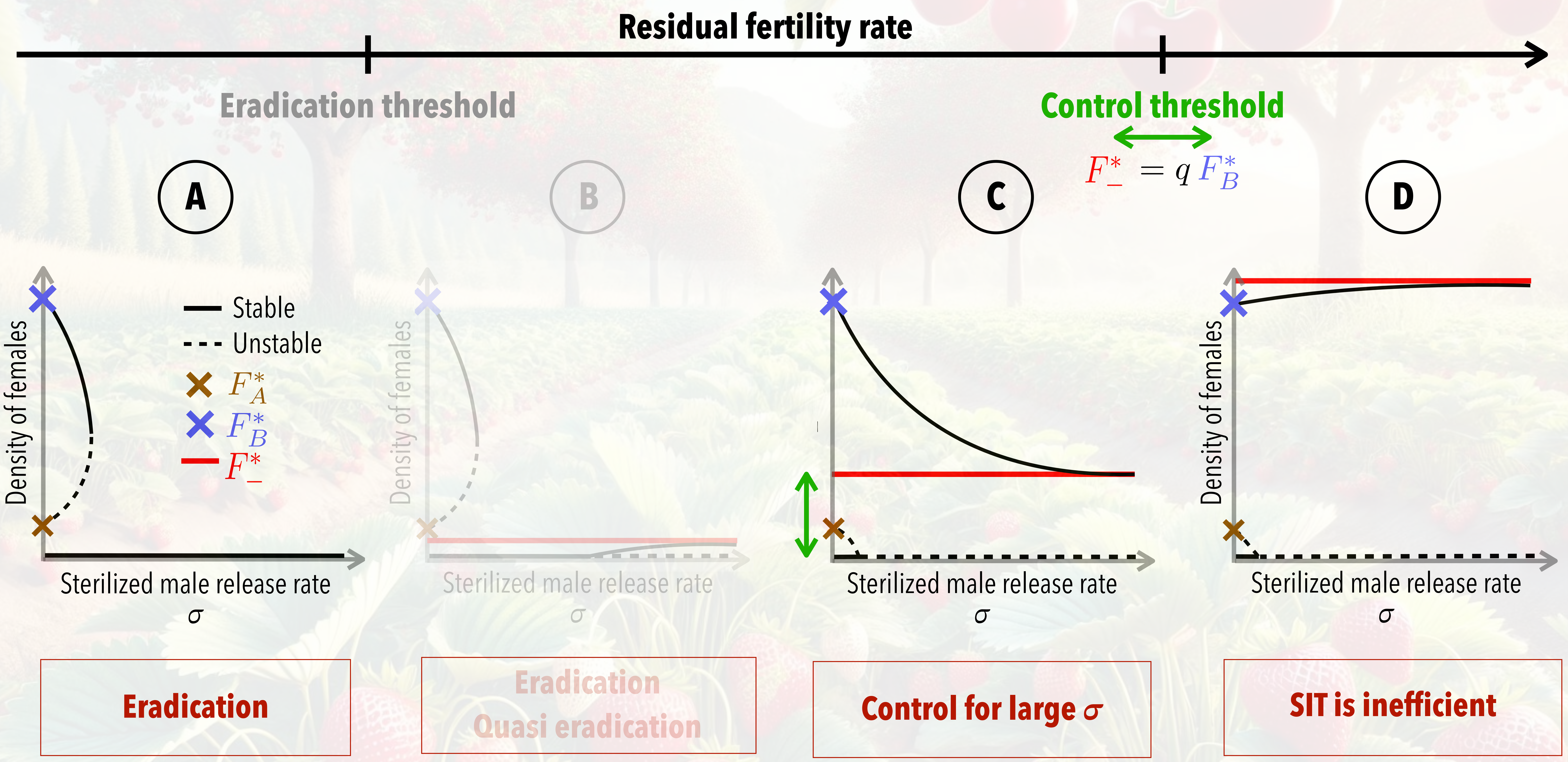
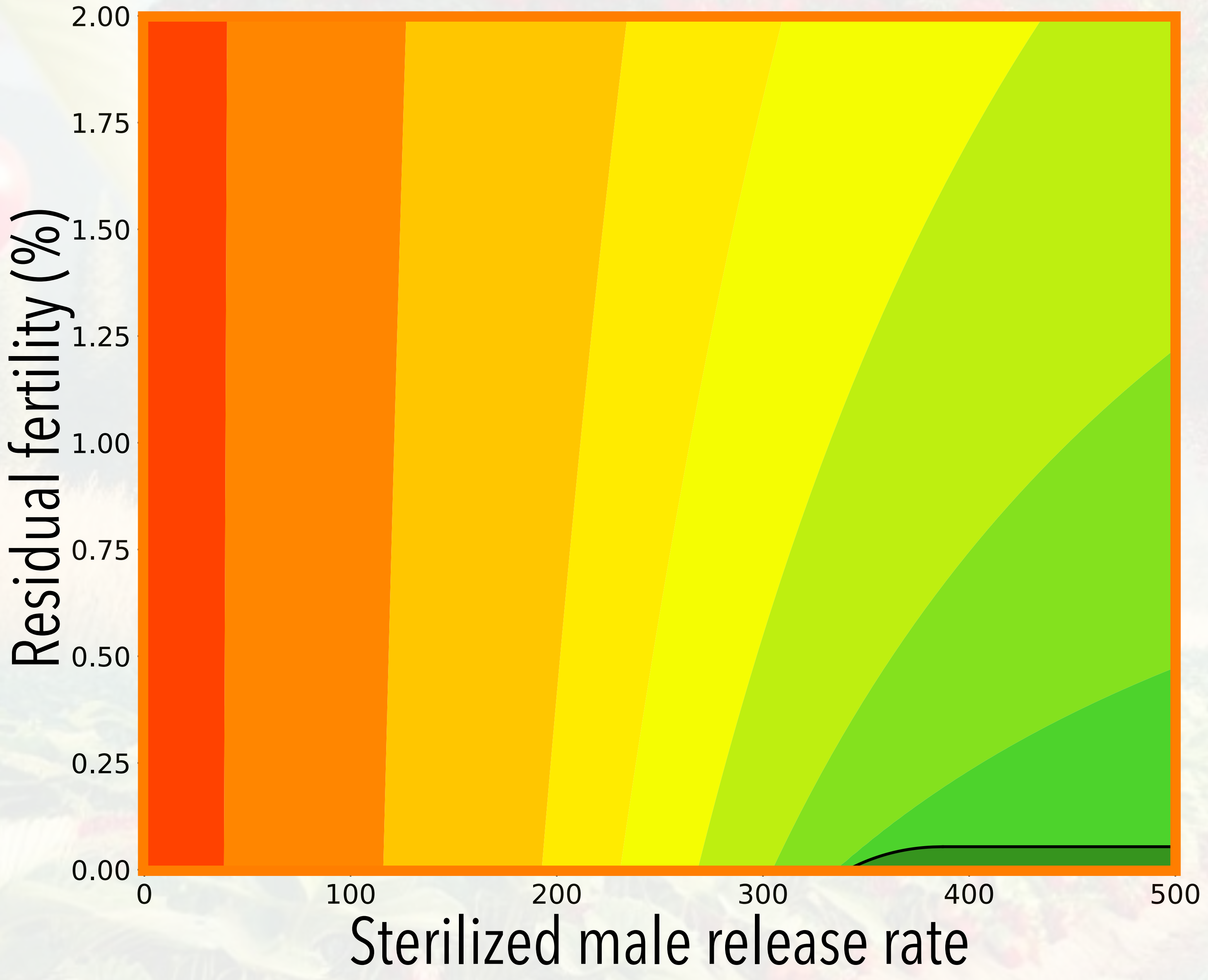


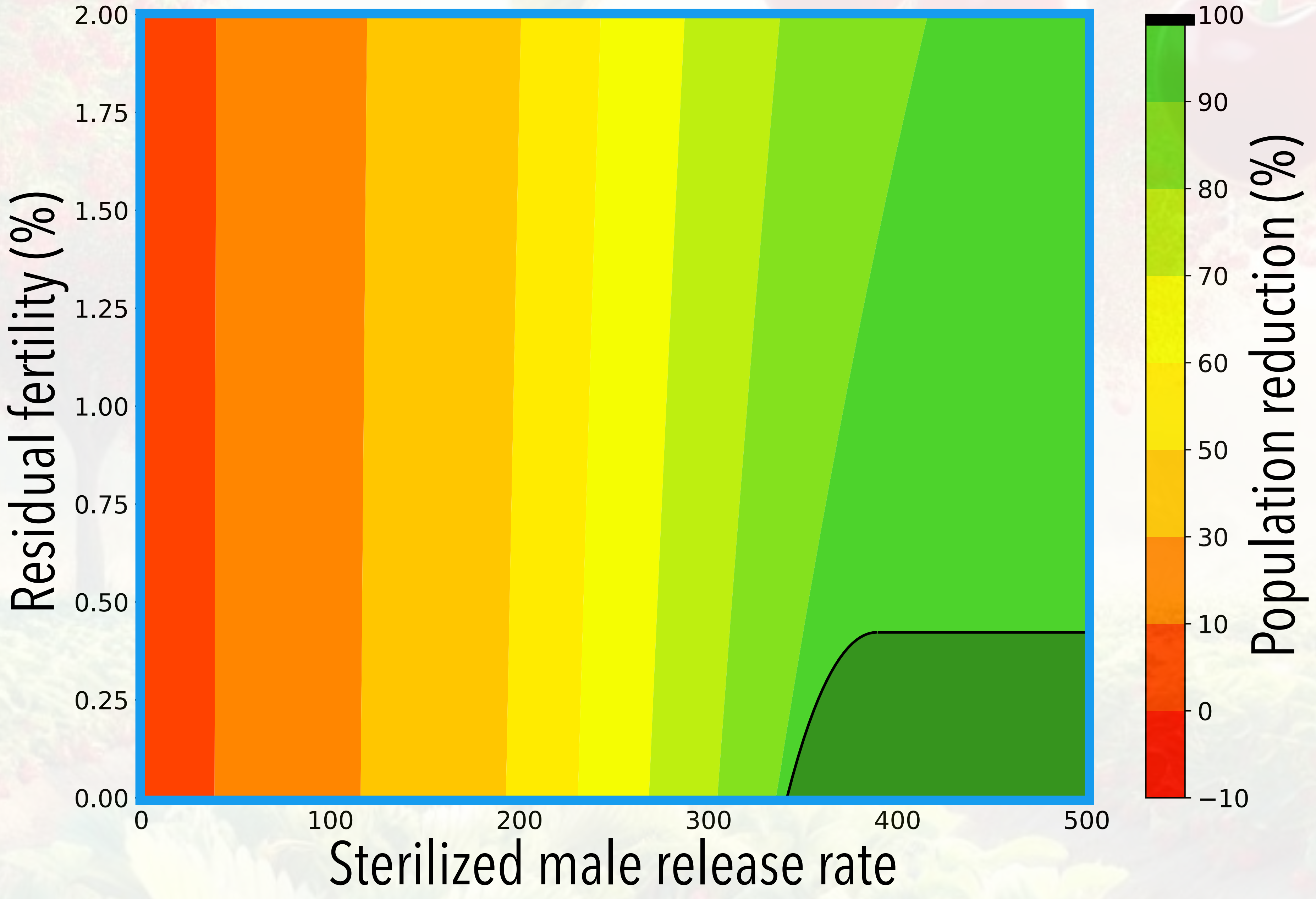
Residual Fertility (RF): Results

How low residual fertility rate should be to ensure pest control?

Cost-free fertility model



Costly fertility model



- SIT allows **pest control** if not eradication
- Pest control is possible even with residual fertility
- **Fitness costs** of fertile released males matter

Ceratitis capitata

Courtois et al. 2024, *Bulletin of Mathematical Biology*

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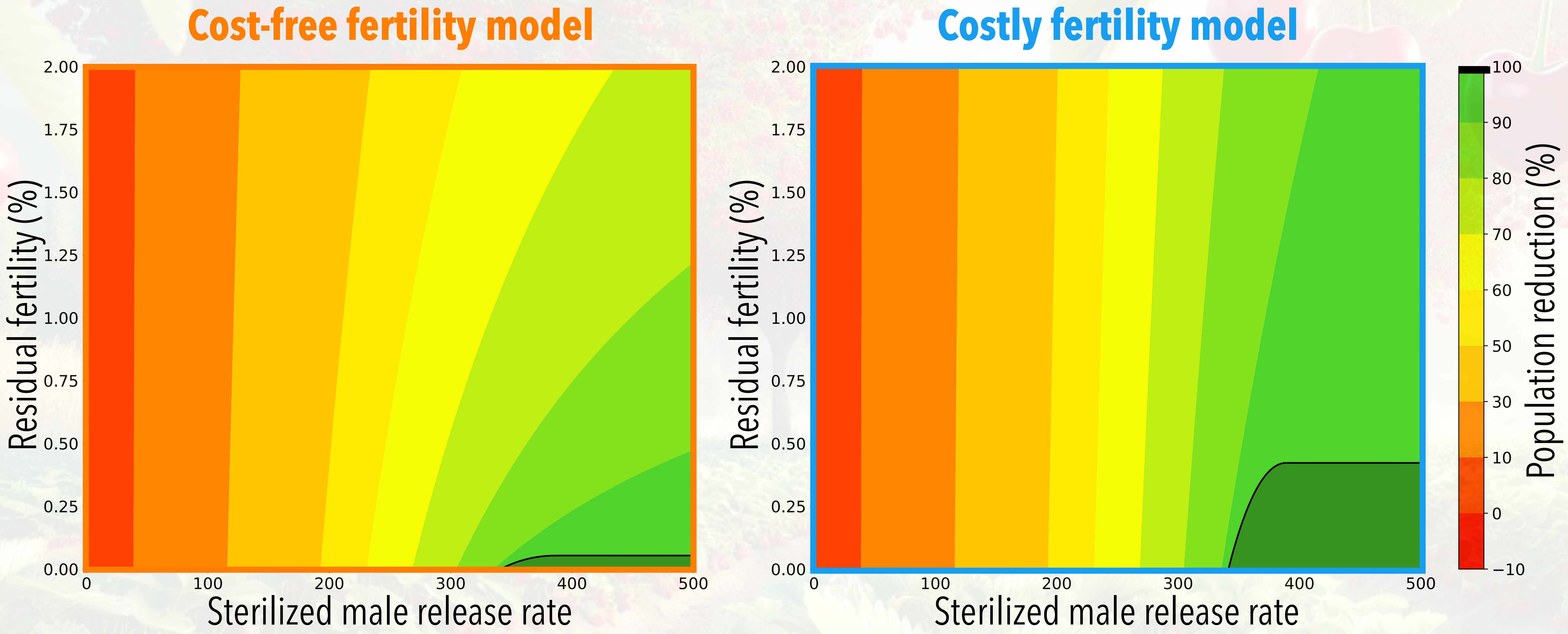

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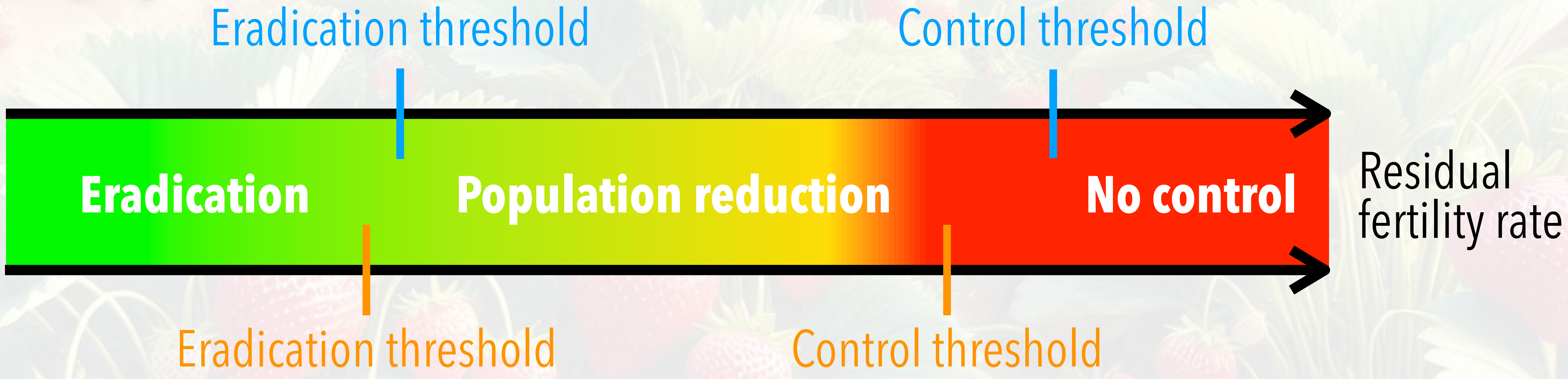

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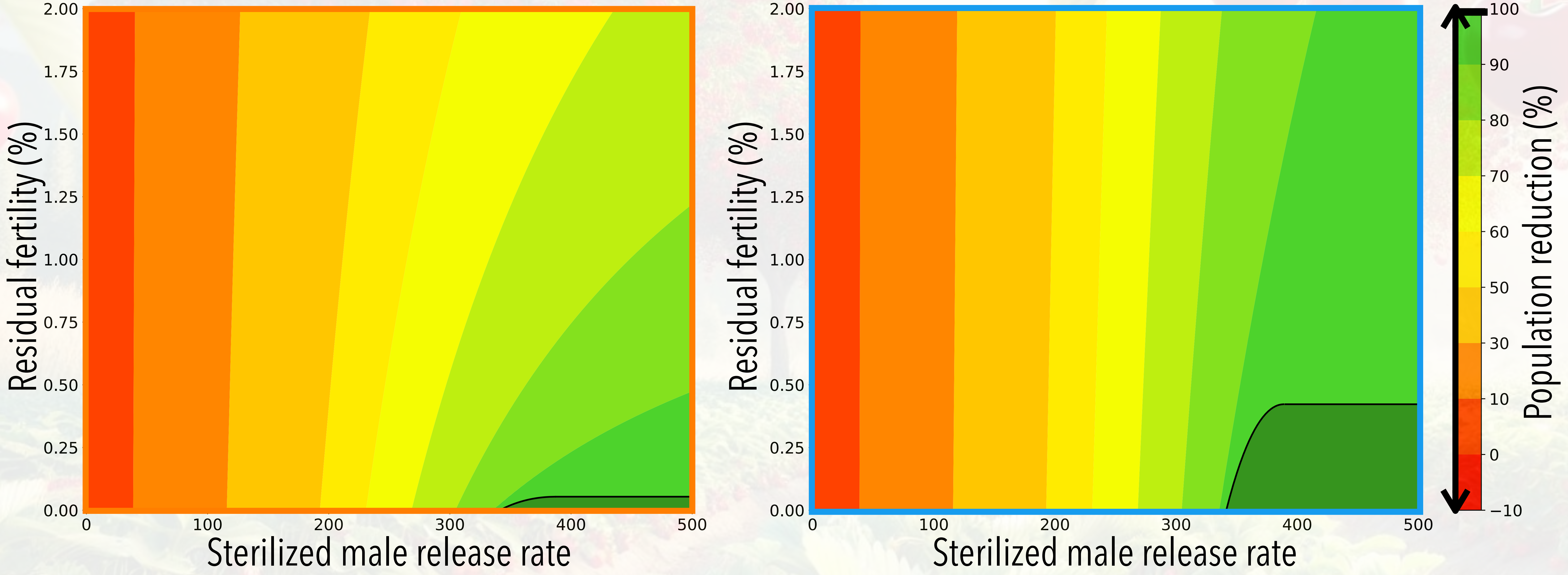

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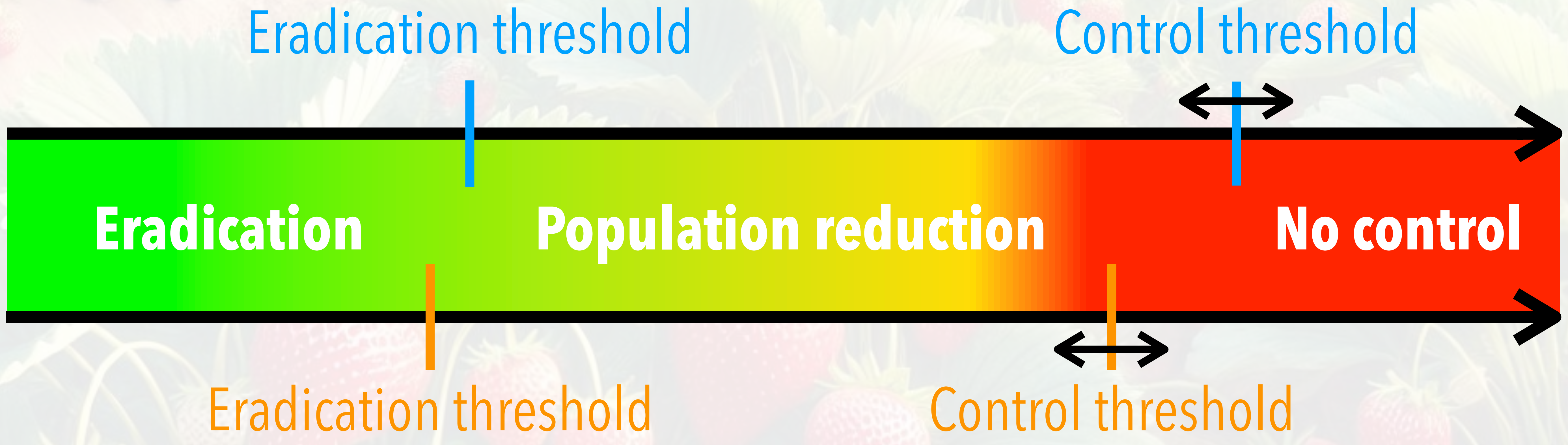

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(2) **Multiple matings**: ability for females to mate and re-mate

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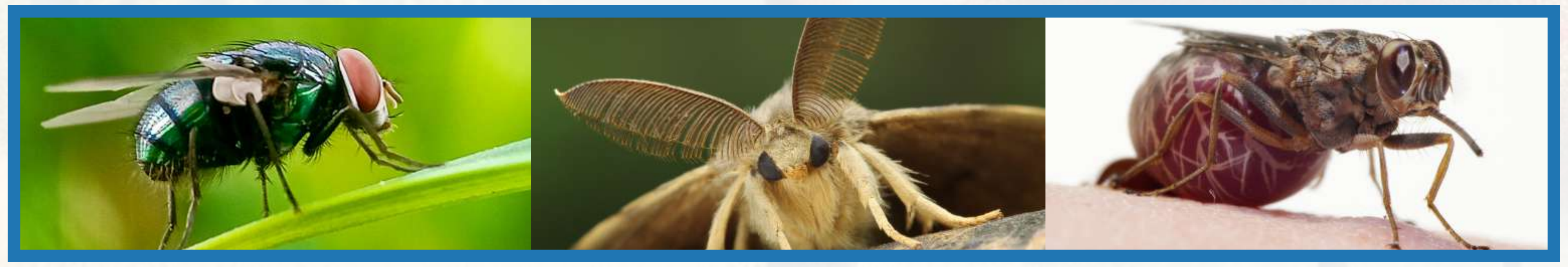
Are multiple matings incompatible with SIT?

Historically...

> **"Females must normally mate only once."** (Knipling, 1955)

New World screwworm *Gypsy moth* *Tsetse fly*



Monoandrous

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New World screwworm *Gypsy moth* *Tsetse fly* *Oriental fruit fly* *Mediterranean fruit fly* *Asian tiger mosquito* *Spotted-wing drosophila*

Monoandrous **Polyandrous**

...but

Polyandry is **not** inherently **incompatible** with SIT (Knipling, 1959a,b; von Borstel and Knipling, 1960; Dyck et al., 2021).

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➪ **However,**

- Female **re-mating rates** and **sperm selection mechanisms** could significantly influence SIT efficiency
  (Pérez-Staples et al, 2013; Vreysen et al, 2007).

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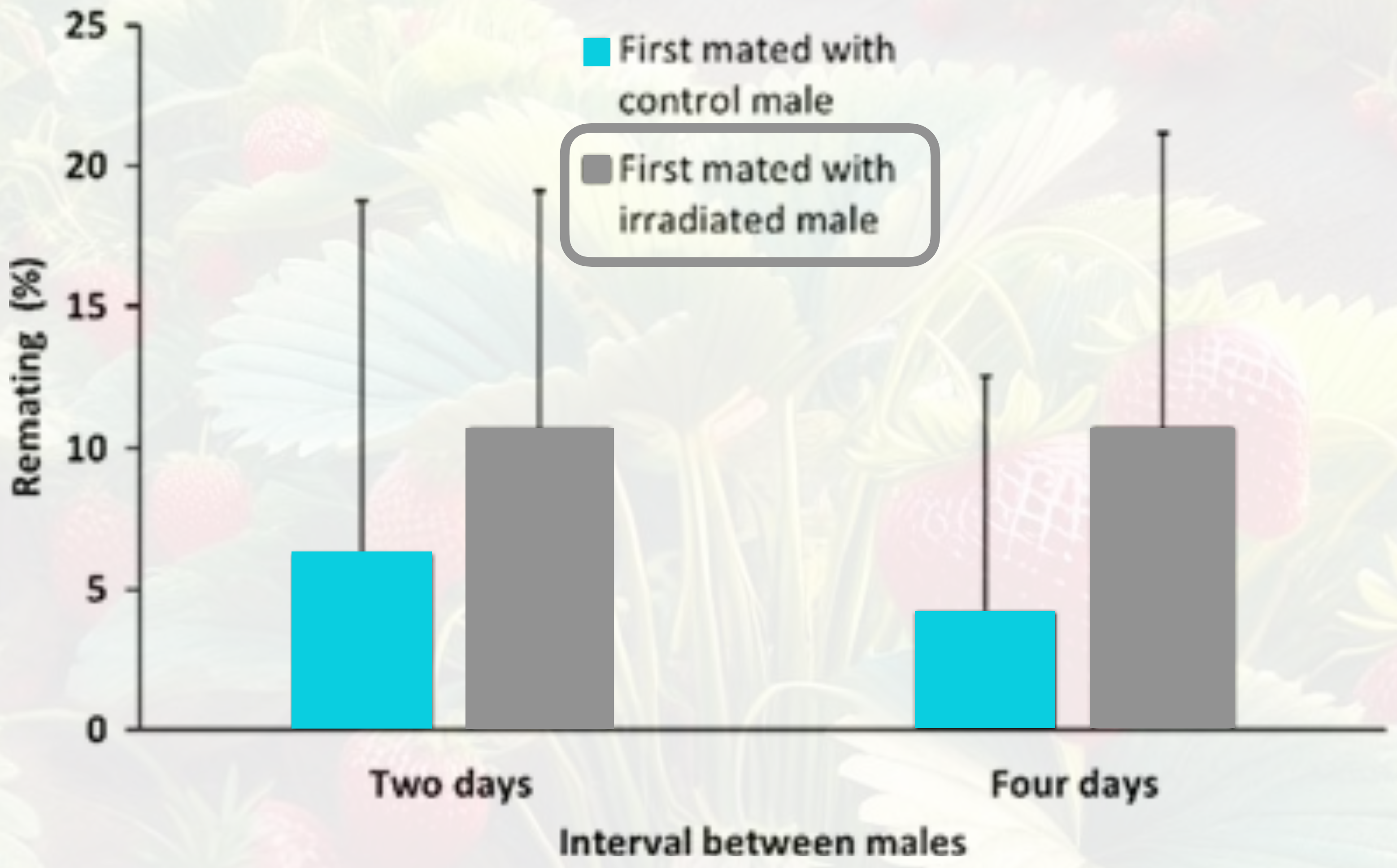
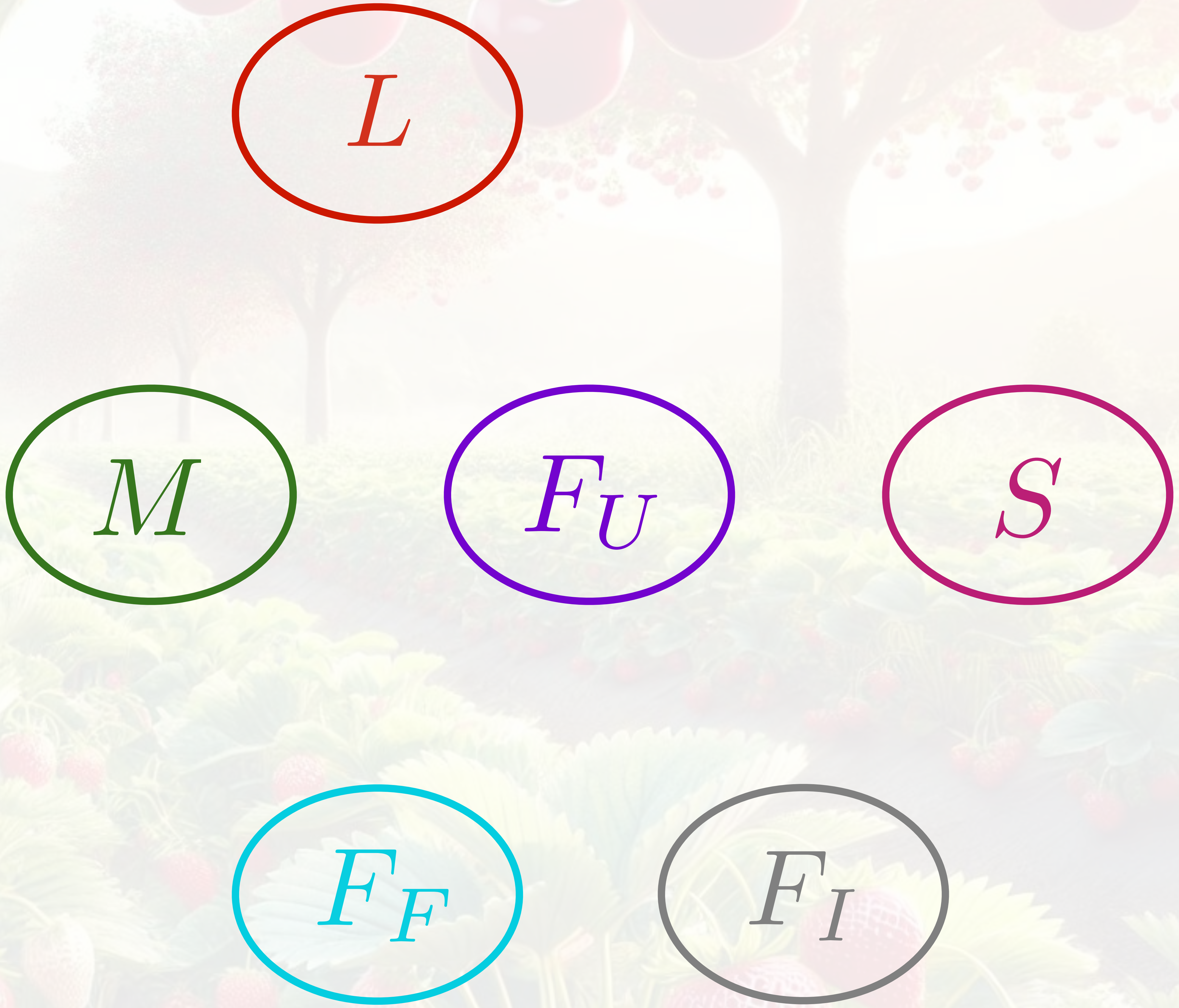


Fig. extracted from Lanouette et al. 2020

(2) **Multiple matings**: ability for females to mate and re-mate

➮ **6 stages:**

- larvae L
- unmated females F_U
- fertilized females F_F
- infertile females F_I
- males M
- sterilized males S

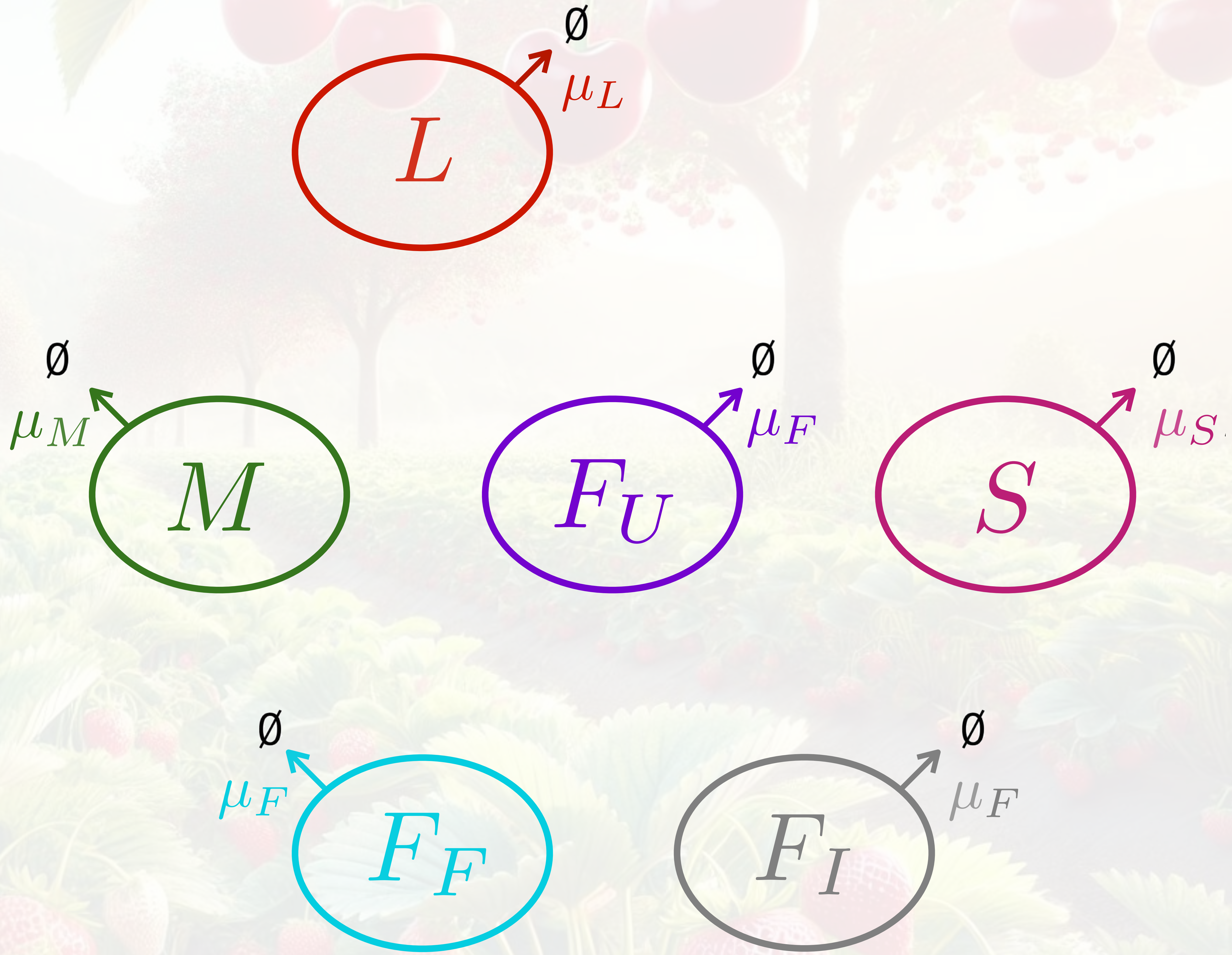


Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

$$
\begin{cases}
\dot{L} = -\mu_L L \\
\dot{M} = -\mu_M M, \\
\dot{F_U} = -\mu_F F_U \\
\dot{F_I} = -\mu_F F_I, \\
\dot{F_F} = -\mu_F F_F, \\
\dot{S} = -\mu_S S
\end{cases}
$$

μ_x Mortality rate



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\dot{F_F} = \chi \frac{M}{M+\eta S} F_U - \mu_F F_F, \\
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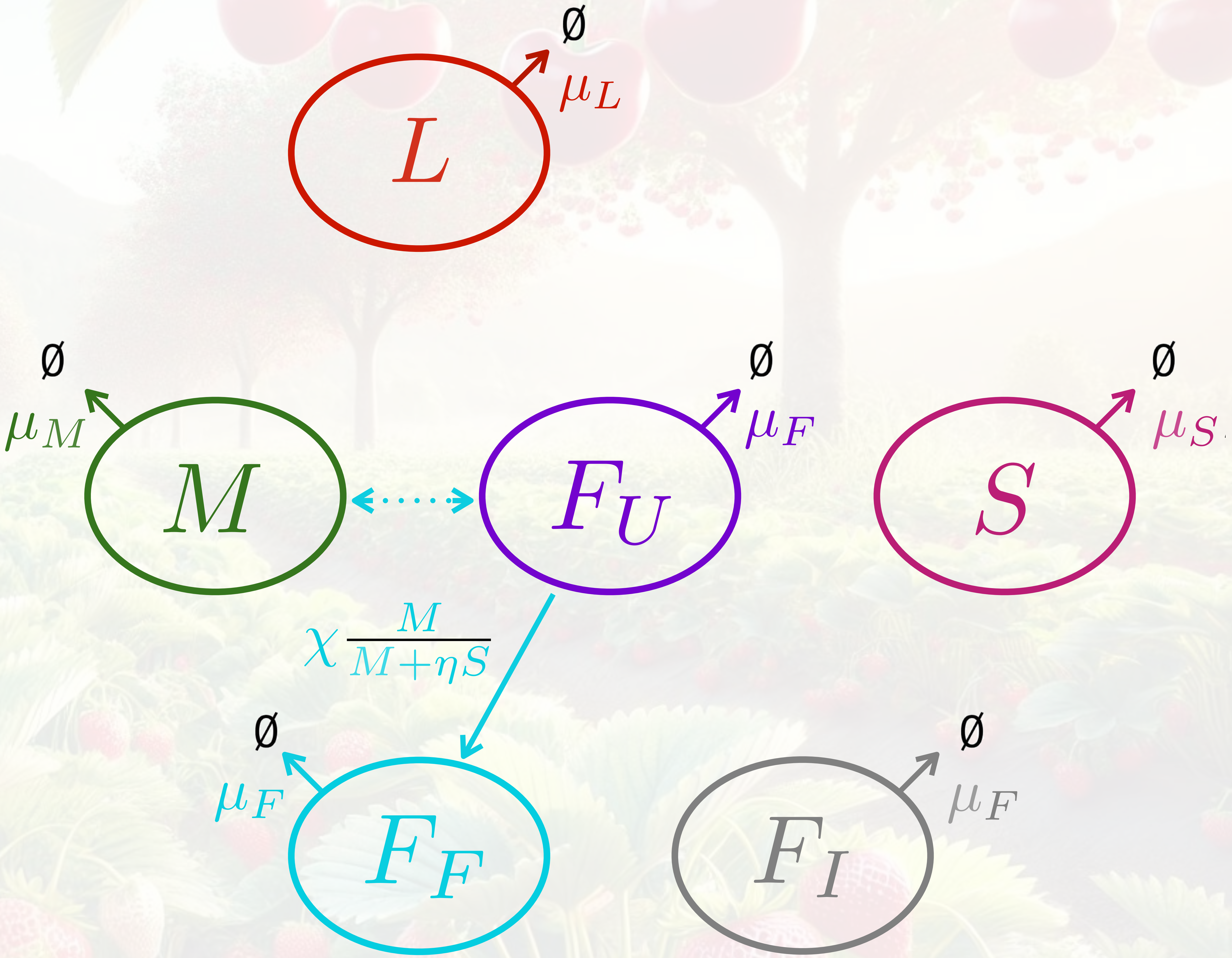
μ_x	Mortality rate
χ	Mating rate
$1-\eta$	Sterilization cost



Drosophila suzukii

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Are multiple matings incompatible with SIT?

$$\begin{cases} \dot{L} = \omega(1 - \frac{L}{K})F_F - \mu_L L \\ \dot{M} = \qquad - \mu_M M, \\ \dot{F_U} = \qquad - \mu_F F_U \\ \dot{F_I} = \qquad - \mu_F F_I, \\ \dot{F_F} = \chi \frac{M}{M+\eta S} F_U \qquad - \mu_F F_F, \\ \dot{S} = -\mu_S S \end{cases}$$

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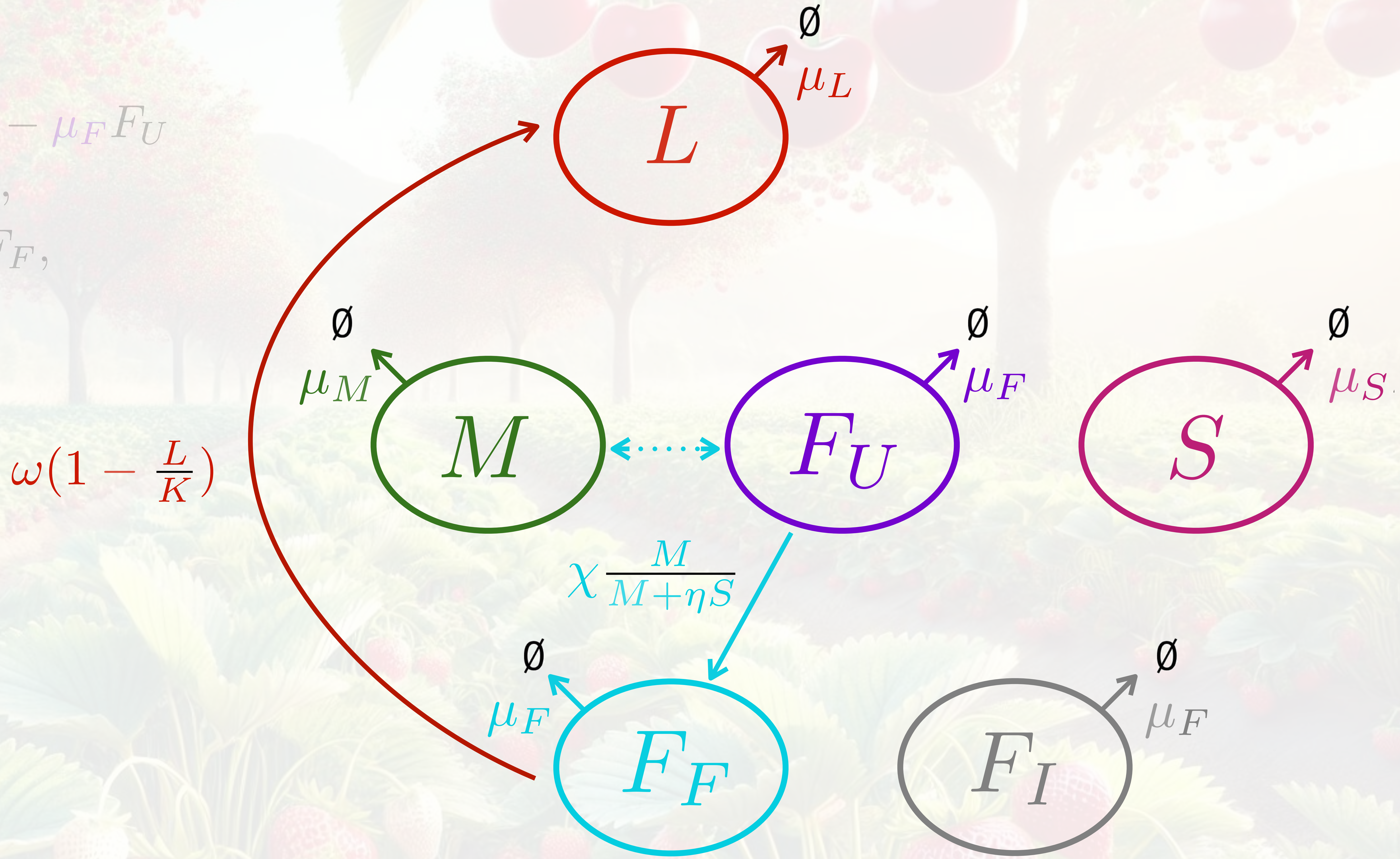
K	Load-carrying capacity



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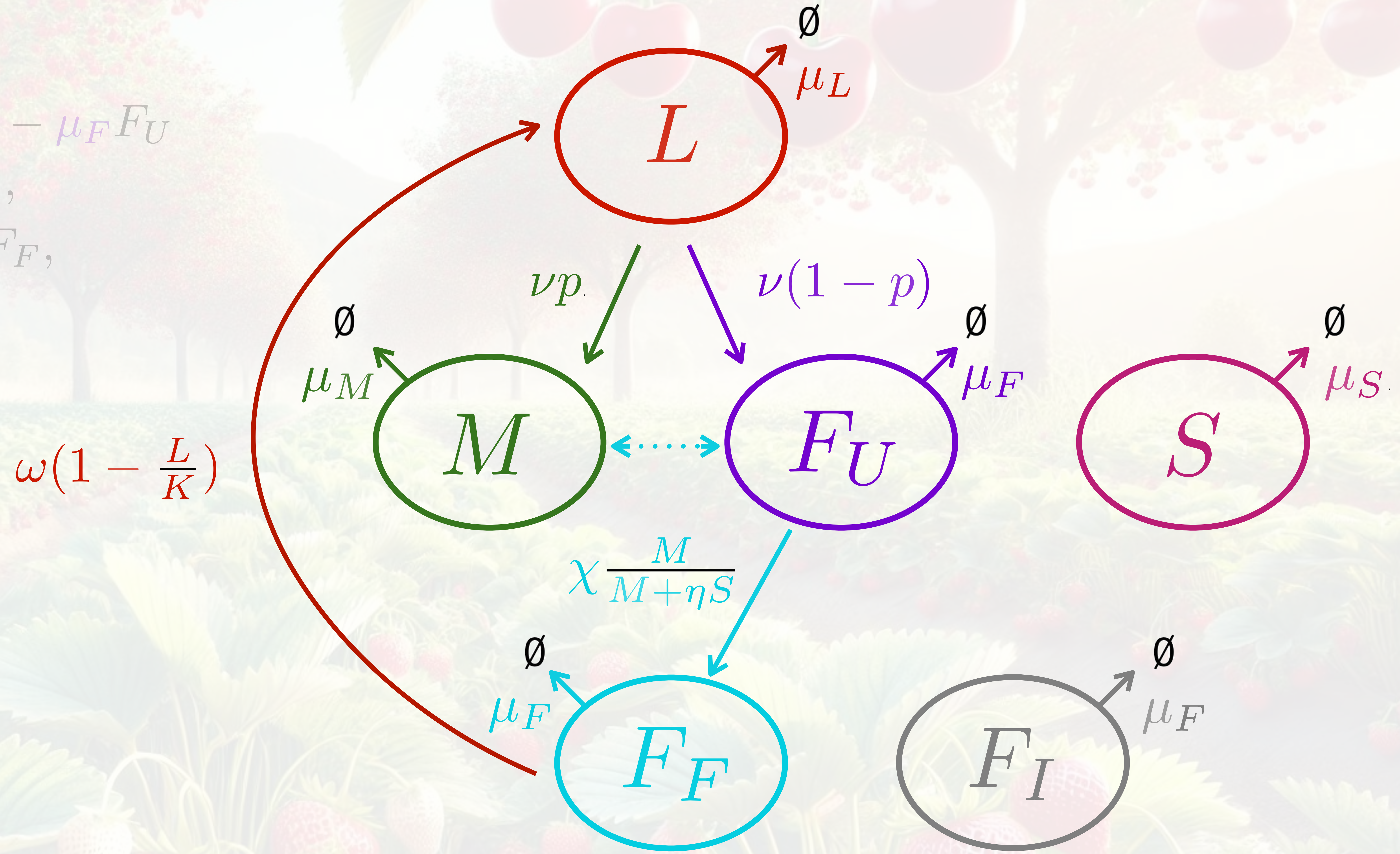

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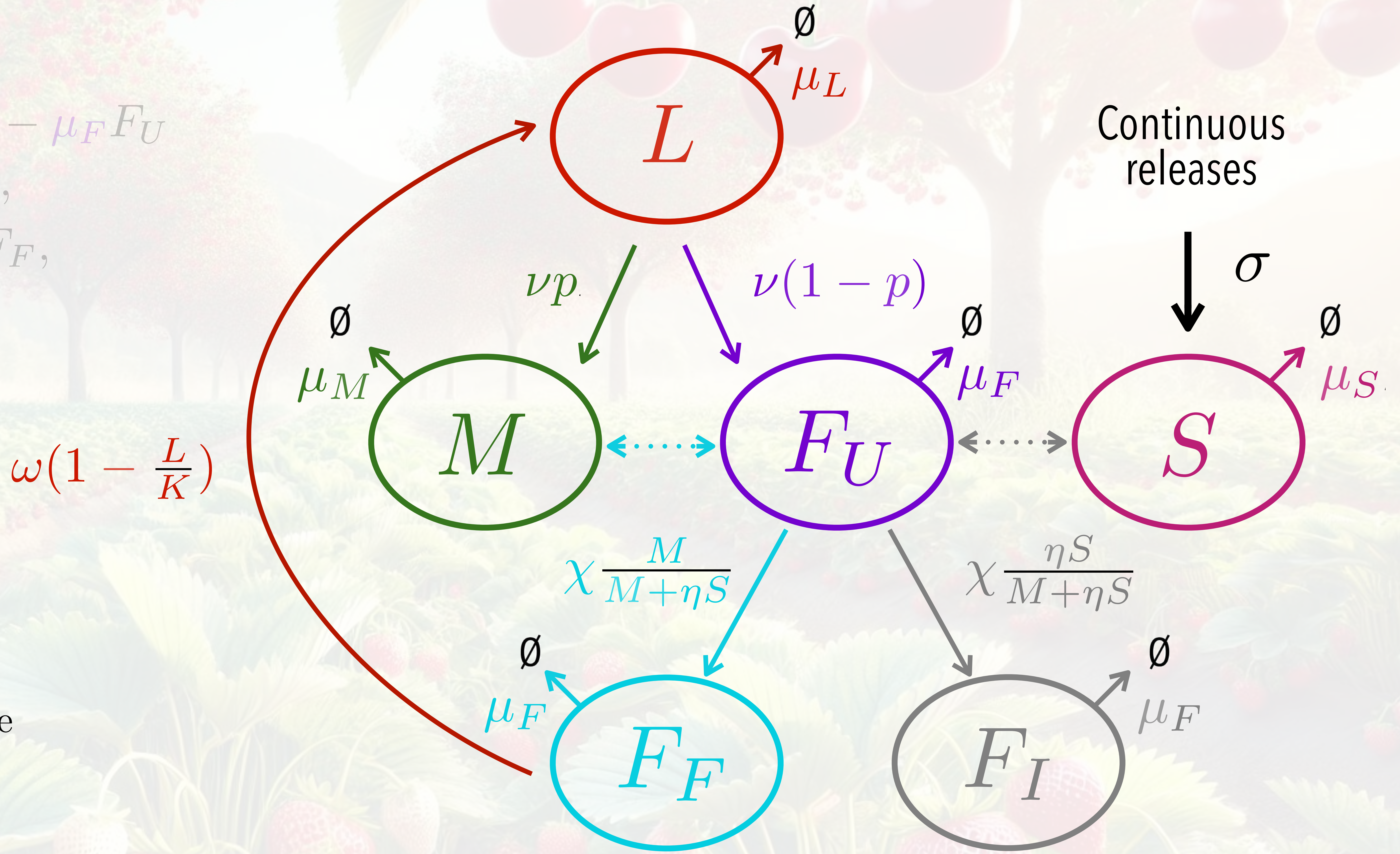

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τ_F	Re-mating rate of "fertilized" females
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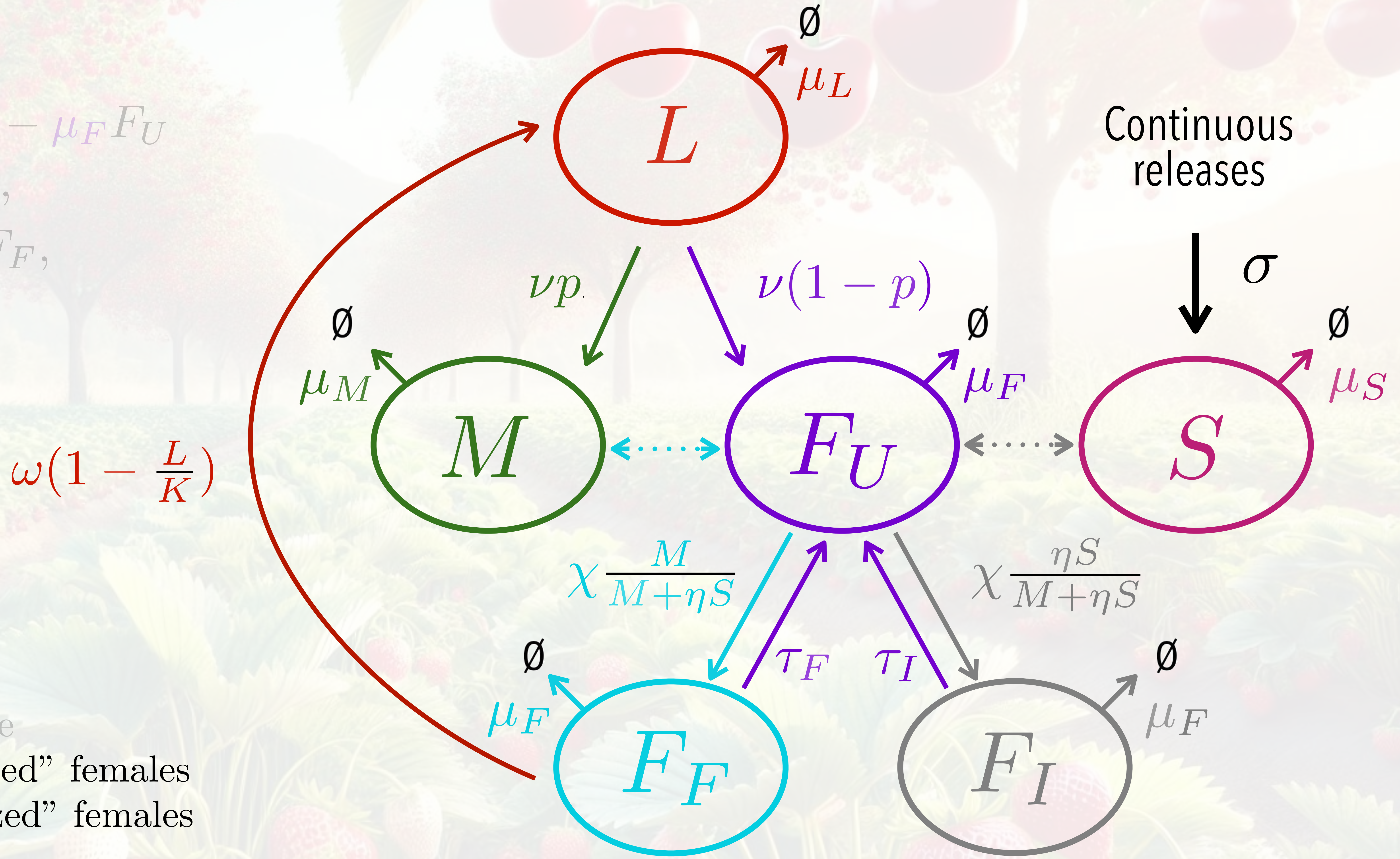

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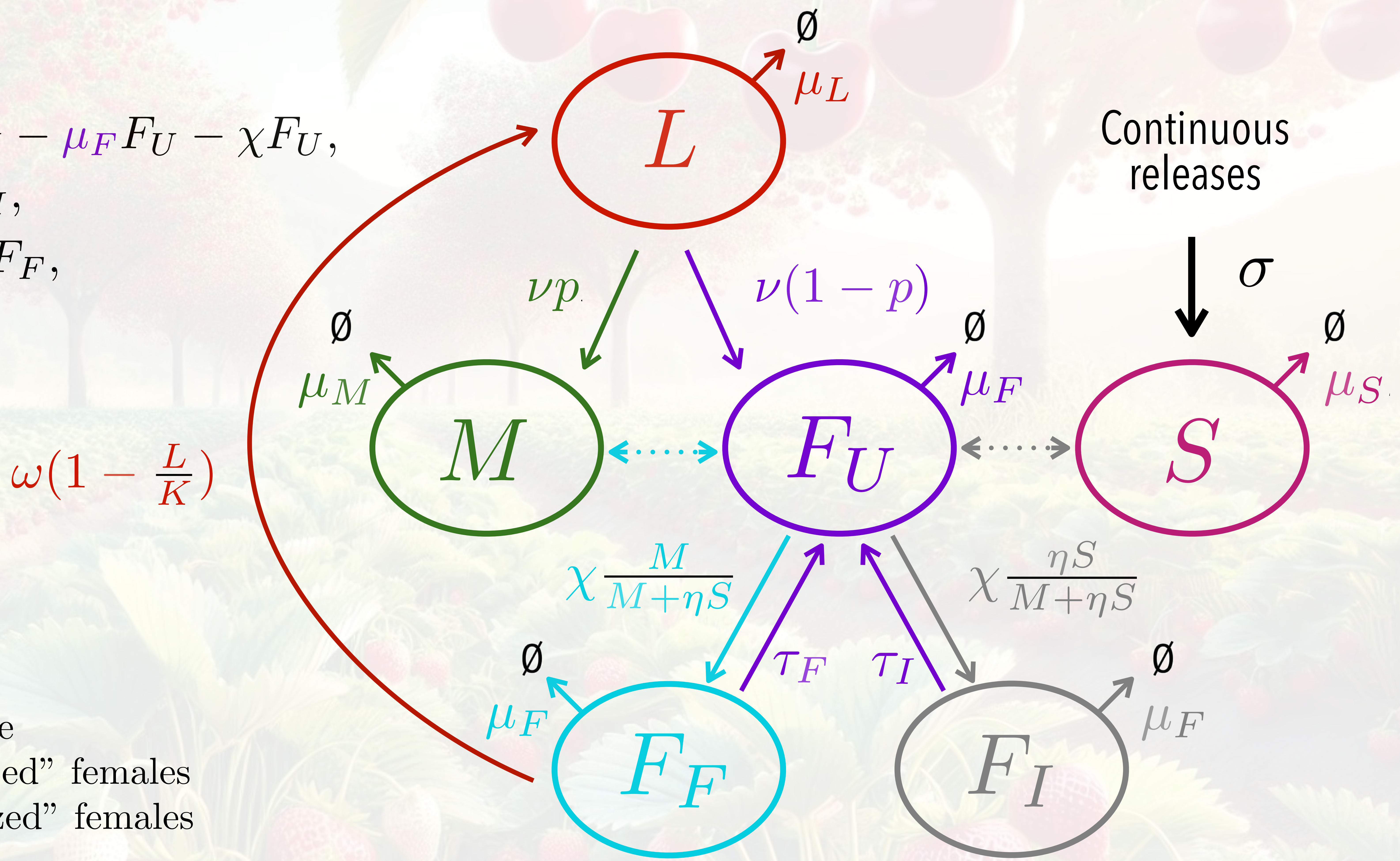

Drosophila suzukii

⇨ **Fertilized females stop laying eggs when they can mate again.**

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

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\dot{L} = \omega(1 - \frac{L}{K})F_F - \mu_L L - \nu L, \\
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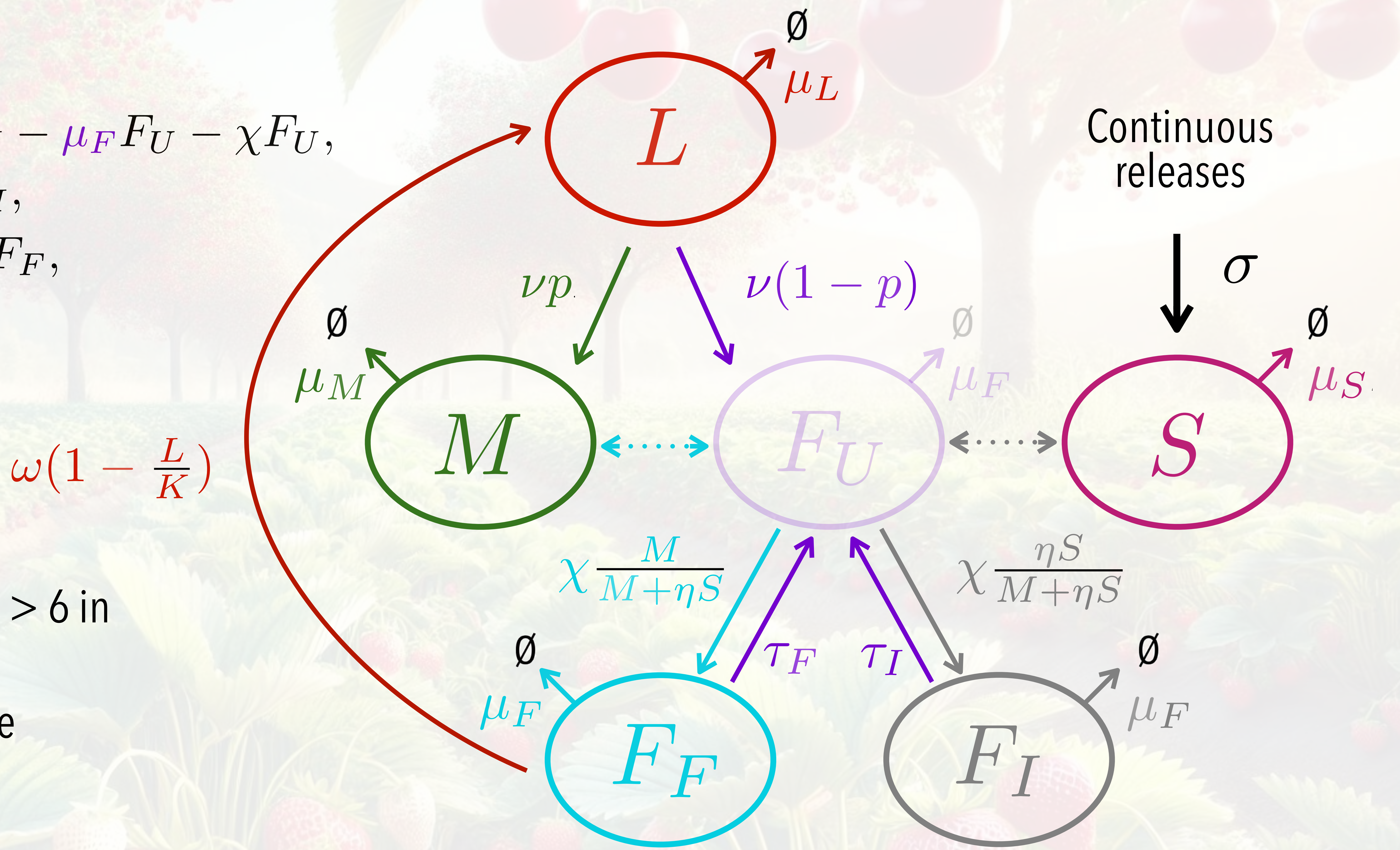

- Non-limiting males, Mating capacity > 6 in 24-hour (Lanouette et al, 2017)
- Female mate shortly after emergence (Revadi et al, 2015)

Drosophila suzukii

- **Slow-fast approximation:** when $\chi \gg$ other parameters

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\dot{F_I} = \underbrace{\nu(1-p)}_{\text{Hatching}}\underbrace{\frac{\eta S}{M+\eta S}}_{\text{Mating}} L + \underbrace{\tau_F \frac{\eta S}{M+\eta S} F_F}_{\text{Remating}} - (\underbrace{\mu_F}_{\text{Mortality}} + \underbrace{\tau_I \frac{M}{M+\eta S}}_{\text{Remating}})F_I, \\
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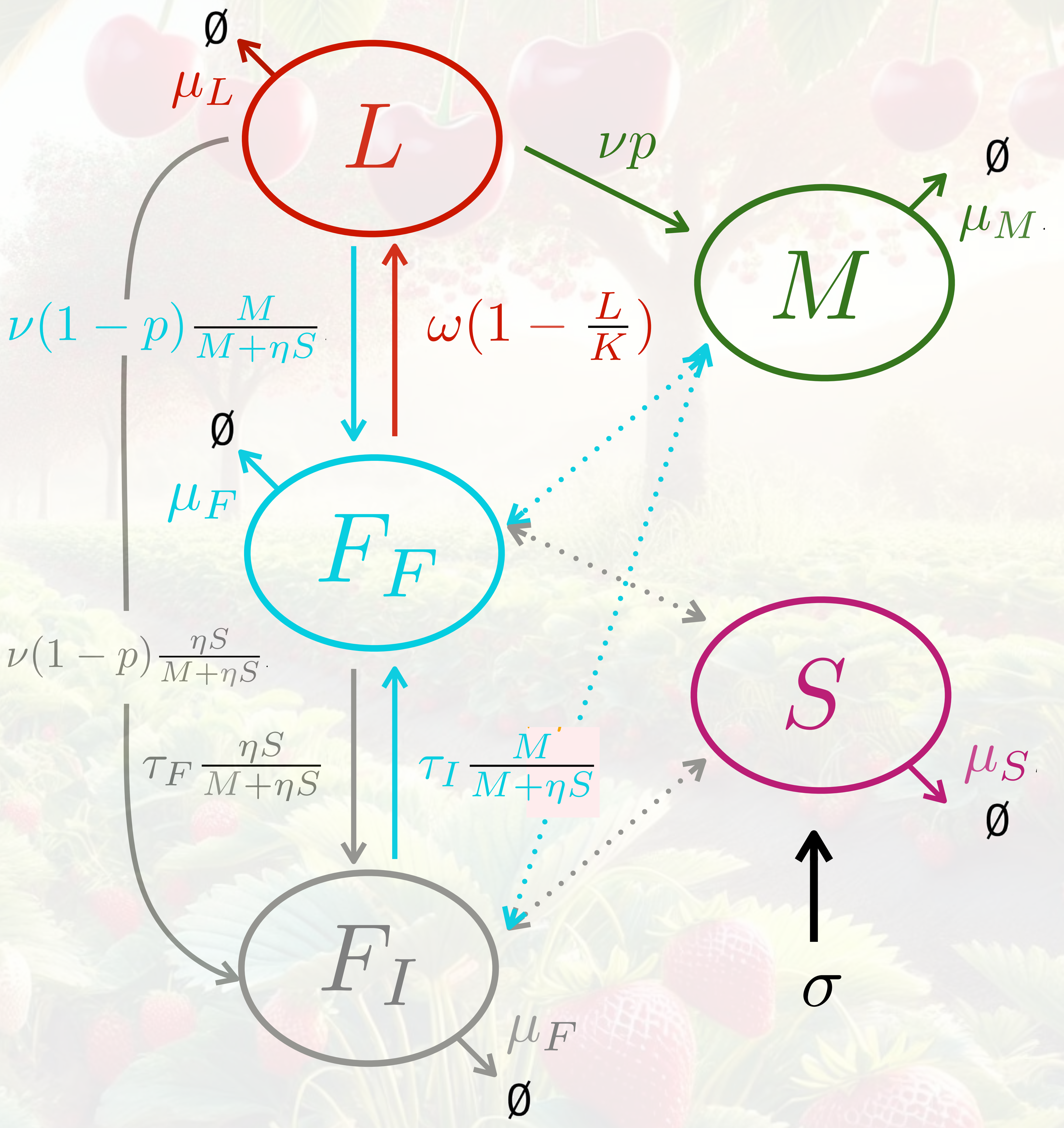

⇨ **Fertilized females lay eggs until they mate with a sterilized male.**

⇨ **Last mating determines offspring**

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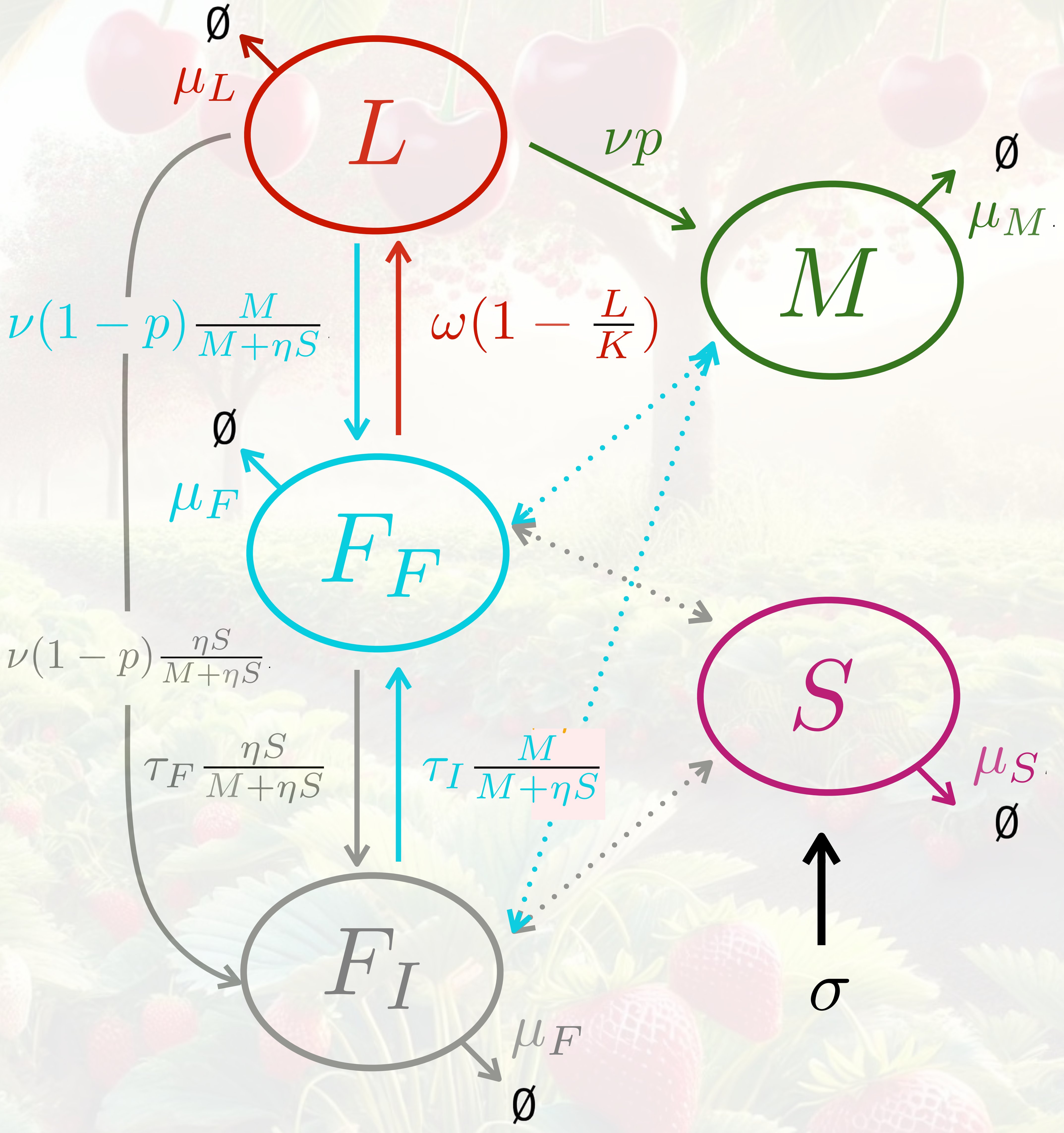

Multiple Matings study:

- **Without MM - First scenario ($\tau_F = \tau_I = 0$)**
- **With MM - Last scenario ($\tau_F > 0, \tau_I > 0$)**

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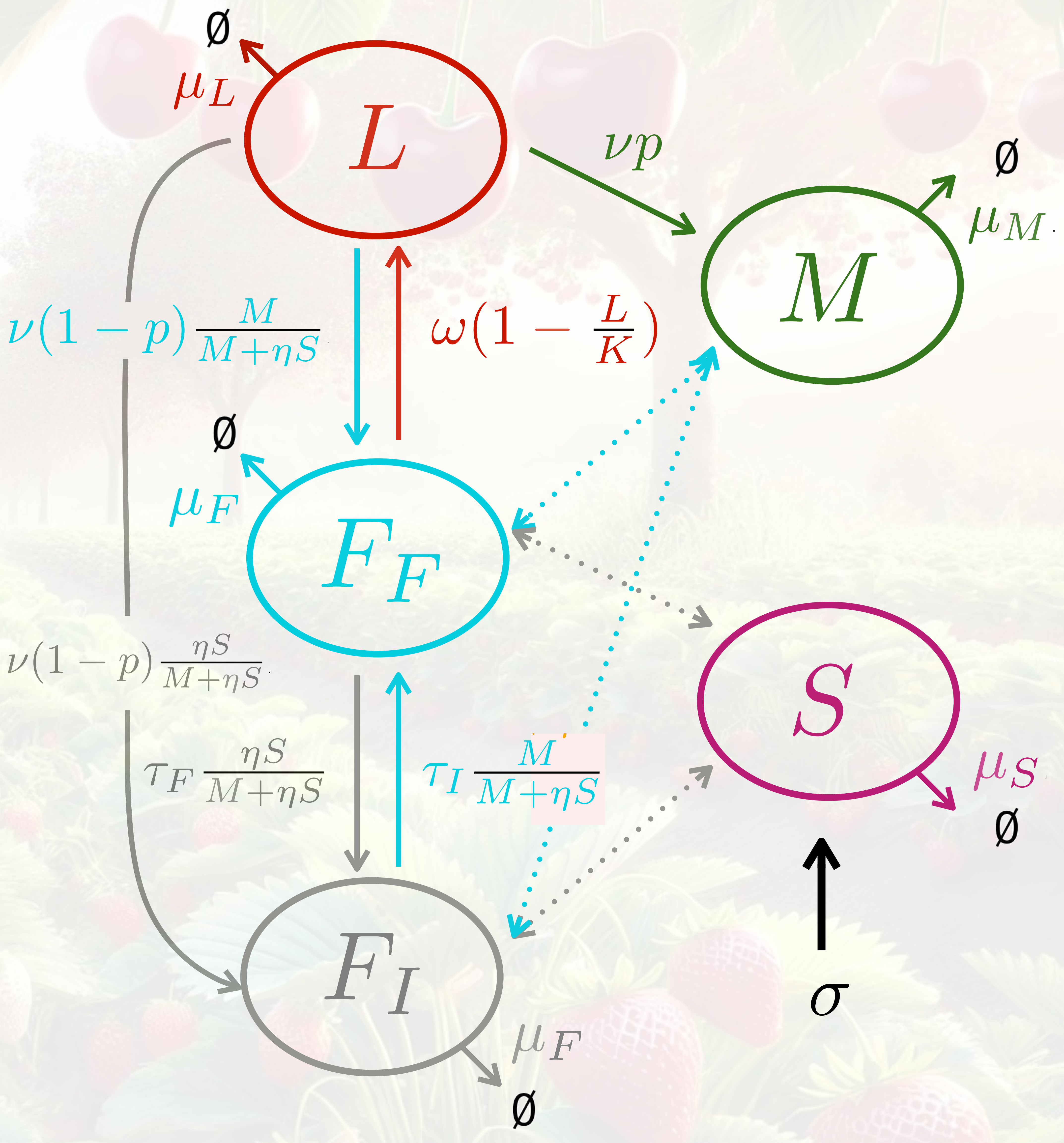
\dot{F_F} = \nu(1-p)\frac{M}{M+\eta S}L + \tau_I \frac{M}{M+\eta S}F_I - (\mu_F + \tau_F \frac{\eta S}{M+\eta S})F_F, \\
\dot{S} = -\mu_S S + \sigma.
\end{cases}
$$

- $\dot{L}$: Egg production | Mortality | Hatching
- $\dot{M}$: Hatching | Mortality
- $\dot{F_I}$: Hatching | Mating | Remating | Mortality | Remating
- $\dot{F_F}$: Hatching | Mating | Remating | Mortality | Remating
- $\dot{S}$: Mortality | Sterilized male releases



<u>Multiple Matings study:</u>

- **Without MM - First scenario ($\tau_F = \tau_I = 0$)**
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⇨ Equilibrium research, Stability study

Are multiple matings incompatible with SIT?

➩ **Equilibria** are solutions of:

$$\begin{cases} F_F = \frac{(\mu_L+\nu)}{\omega(1-\frac{L}{K})}L, & \text{(i)} \\ M = \frac{\nu p}{\mu_M}L = \gamma L, & \text{(ii)} \\ F_I = (\frac{\nu(1-p)}{\mu_F} - \frac{(\mu_L+\nu)}{\omega(1-\frac{L}{K})})L, & \text{(iii)} \\ \nu(1-p)\frac{\eta S}{M+\eta S}F_F + \tau_F\frac{\eta S}{M+\eta S}F_F - (\mu_F + \tau_I\frac{M}{M+\eta S})F_I = 0, & \text{(iv)} \\ S = \frac{\sigma}{\mu_S}. & \text{(v)} \end{cases}$$

Basic reproduction number

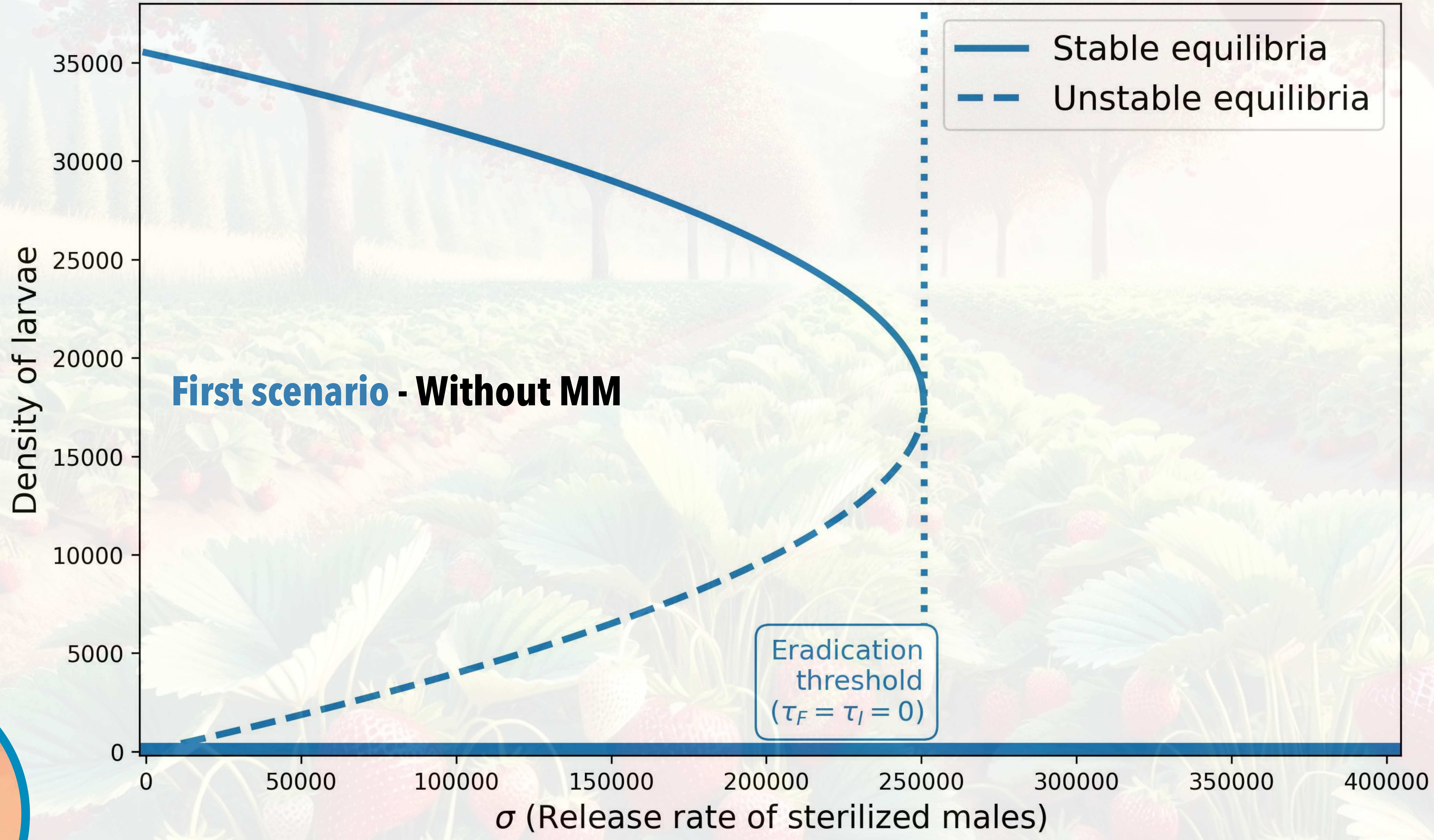
$$\mathcal{R}_0 = \frac{\nu(1-p)\omega}{\mu_F(\mu_L+\nu)} > 1$$

- **Pest-free equilibrium:** $E_0^* = (0, 0, 0, 0, \frac{\sigma}{\mu_S})$
- **Infestation equilibria:** using (i), (ii), (iii), (iv) and (v), other equilibria are solutions of:

$$-\frac{\gamma\mu_S(\mu_F+\tau_I)\mathcal{R}_0}{K\eta(\mu_F+\tau_F)}(L^*)^2 + \frac{\gamma\mu_S(\mu_F+\tau_I)(\mathcal{R}_0-1)}{\eta(\mu_F+\tau_F)}L^* = \sigma.$$

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?



Drosophila suzukii

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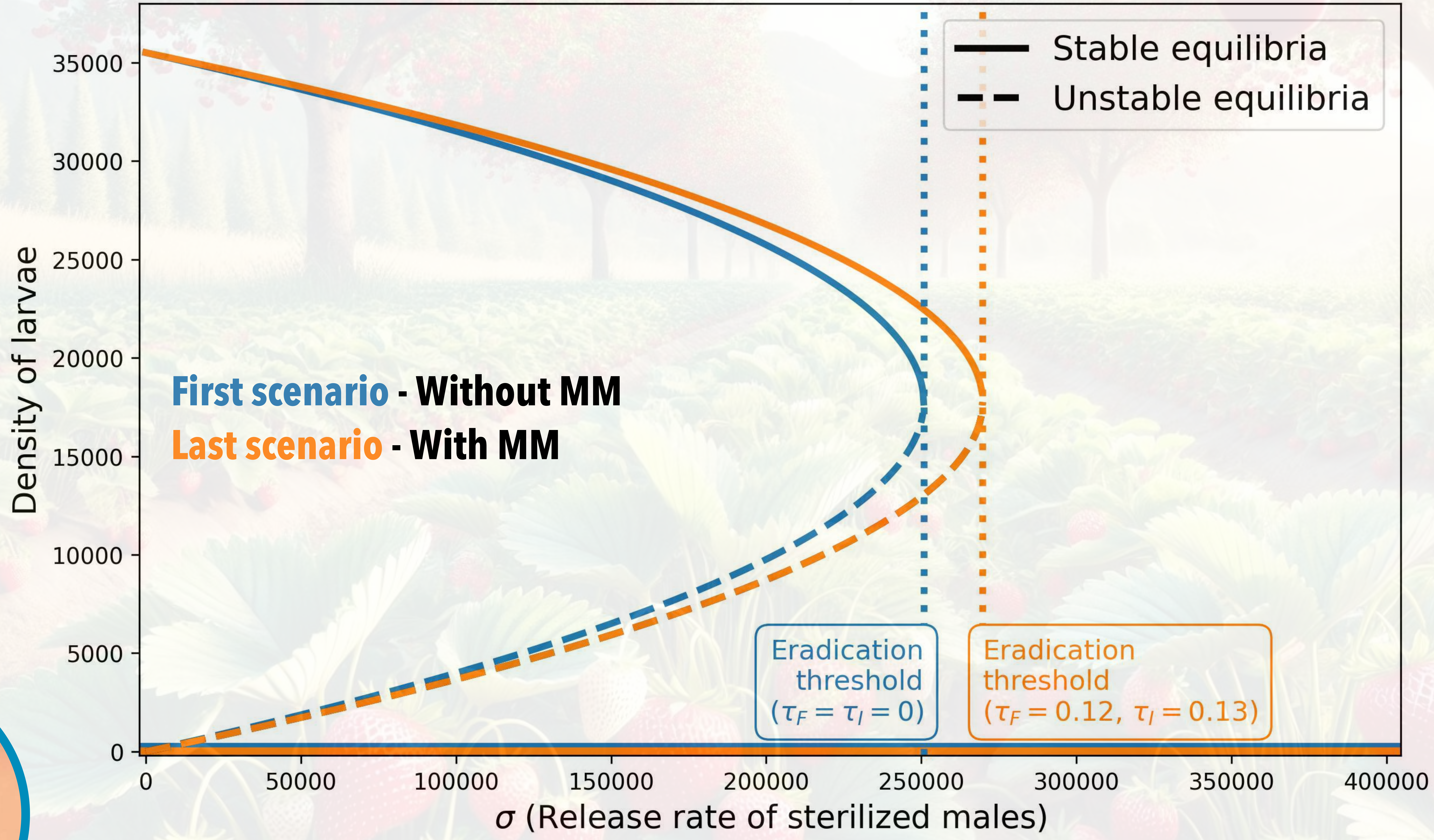

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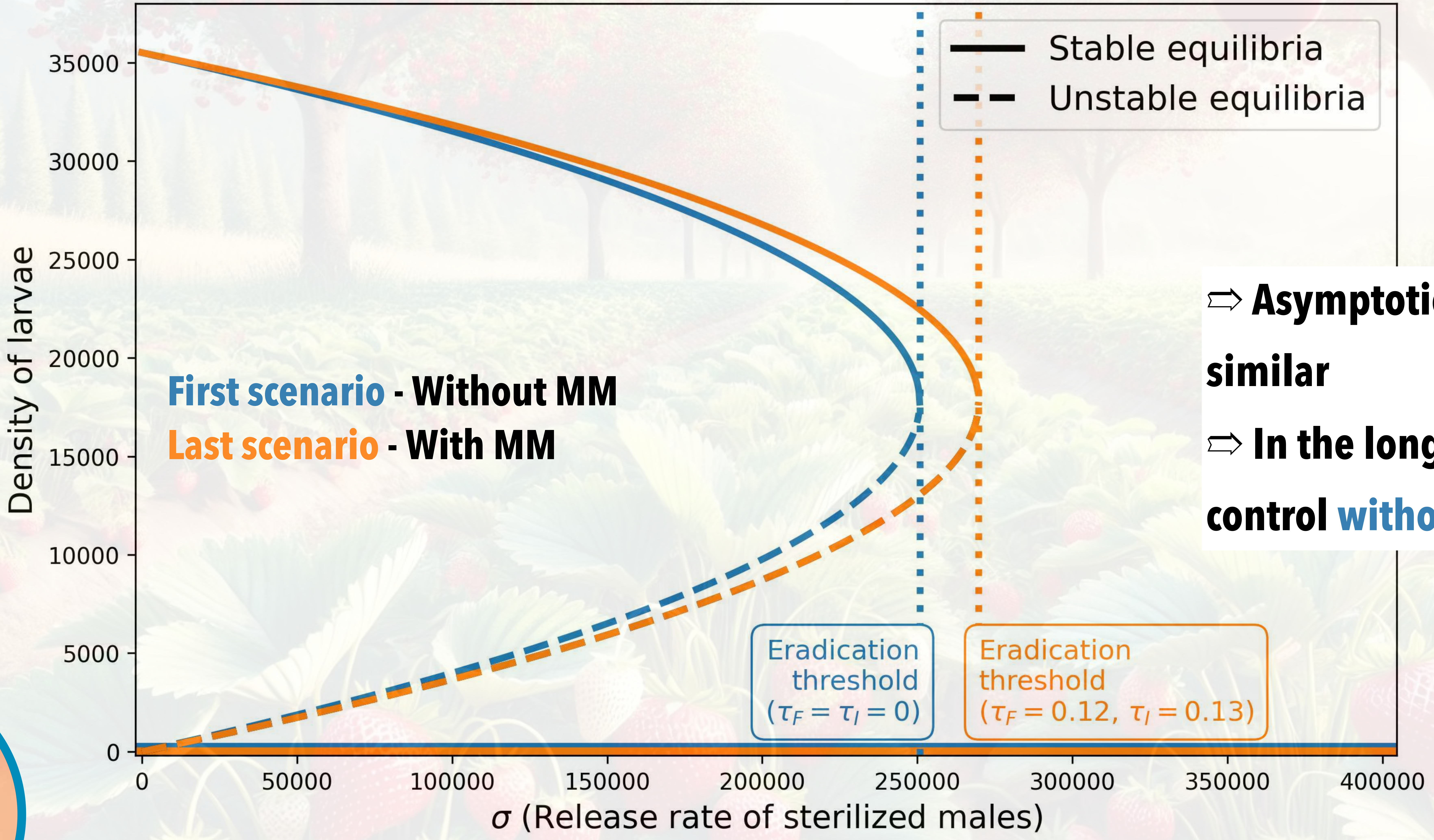

First scenario - Without MM

Last scenario - With MM

⇨ **Asymptotic behavior quite similar**

⇨ **In the long term easier to control without MM**

Drosophila suzukii

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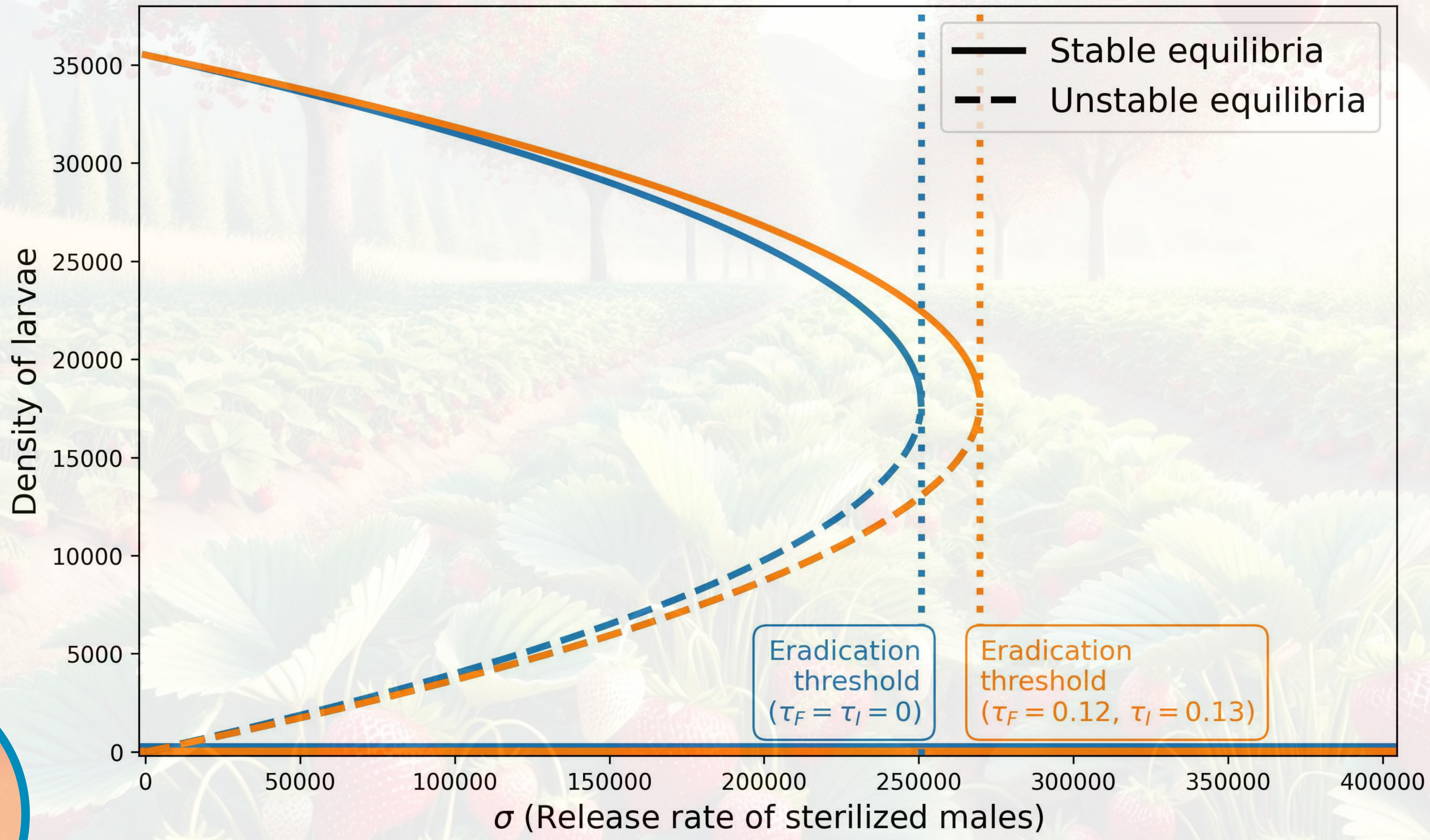
Are multiple matings incompatible with SIT?

Without remating = Equal remating > Remating ($\tau_I > \tau_F$)



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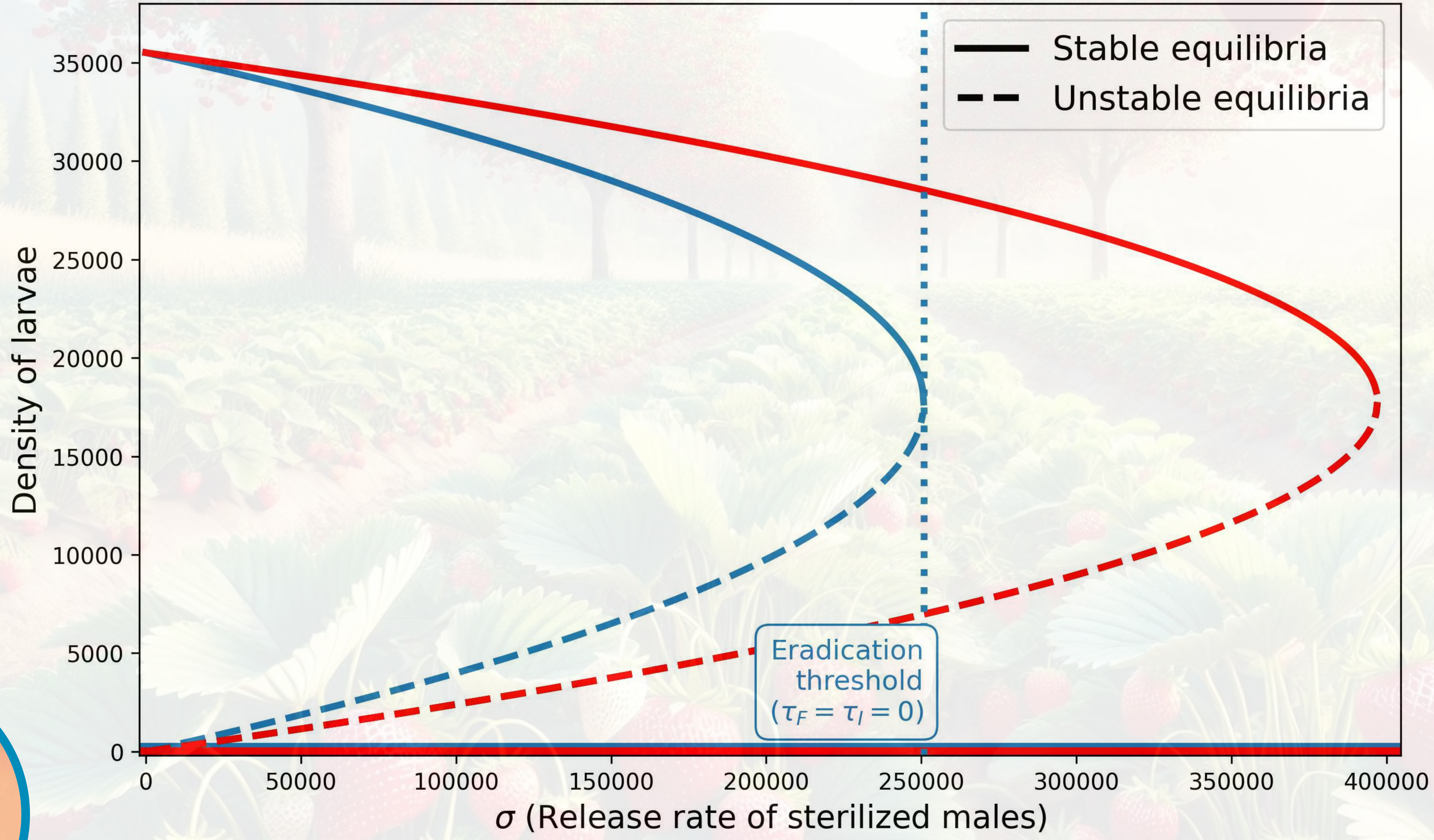
Without remating = Equal remating > Remating ($\tau_I > \tau_F$) > Remating of infertile females only ($\tau_I > \tau_F = 0$)



Drosophila suzukii

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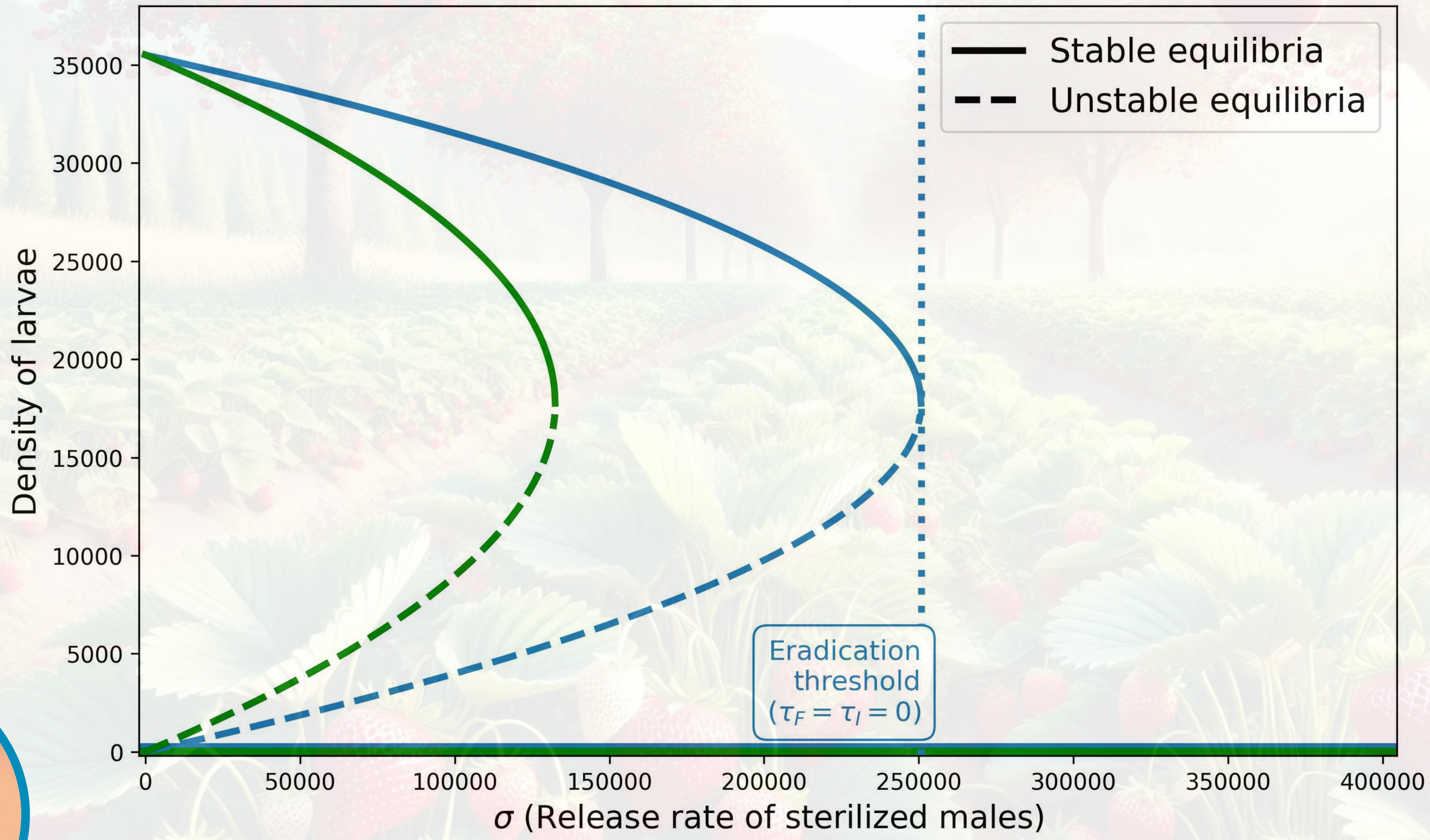

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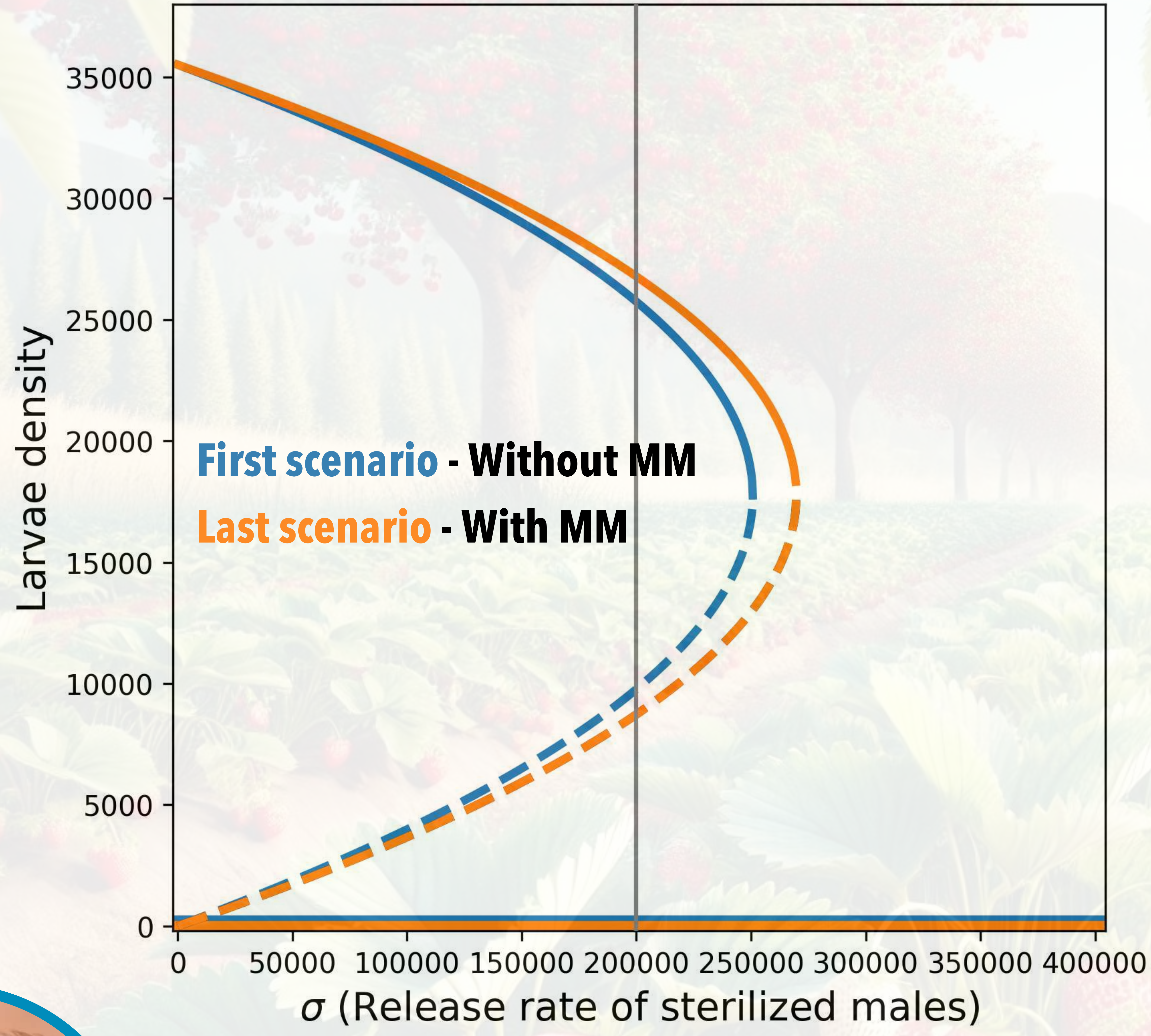

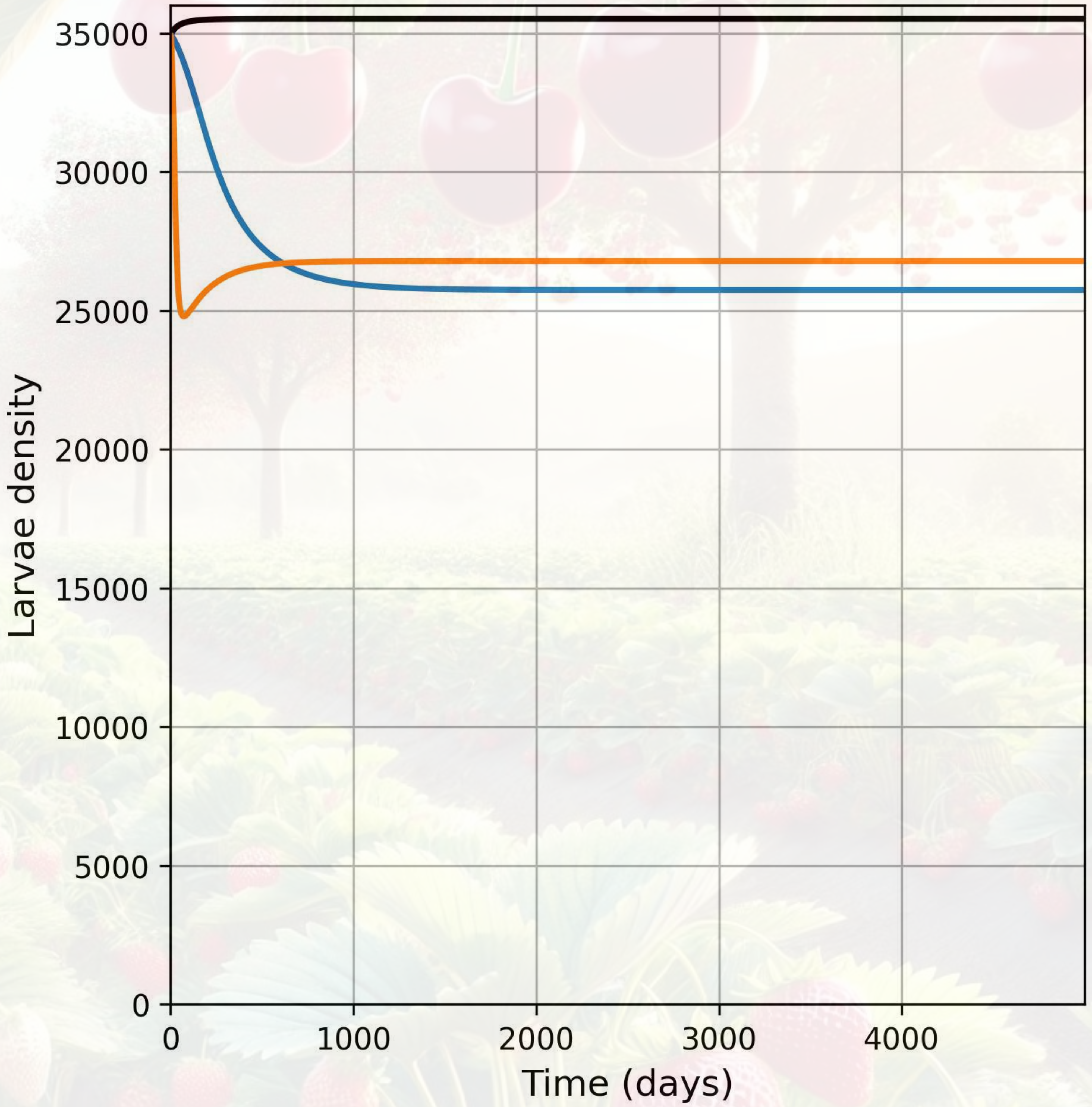

Drosophila suzukii

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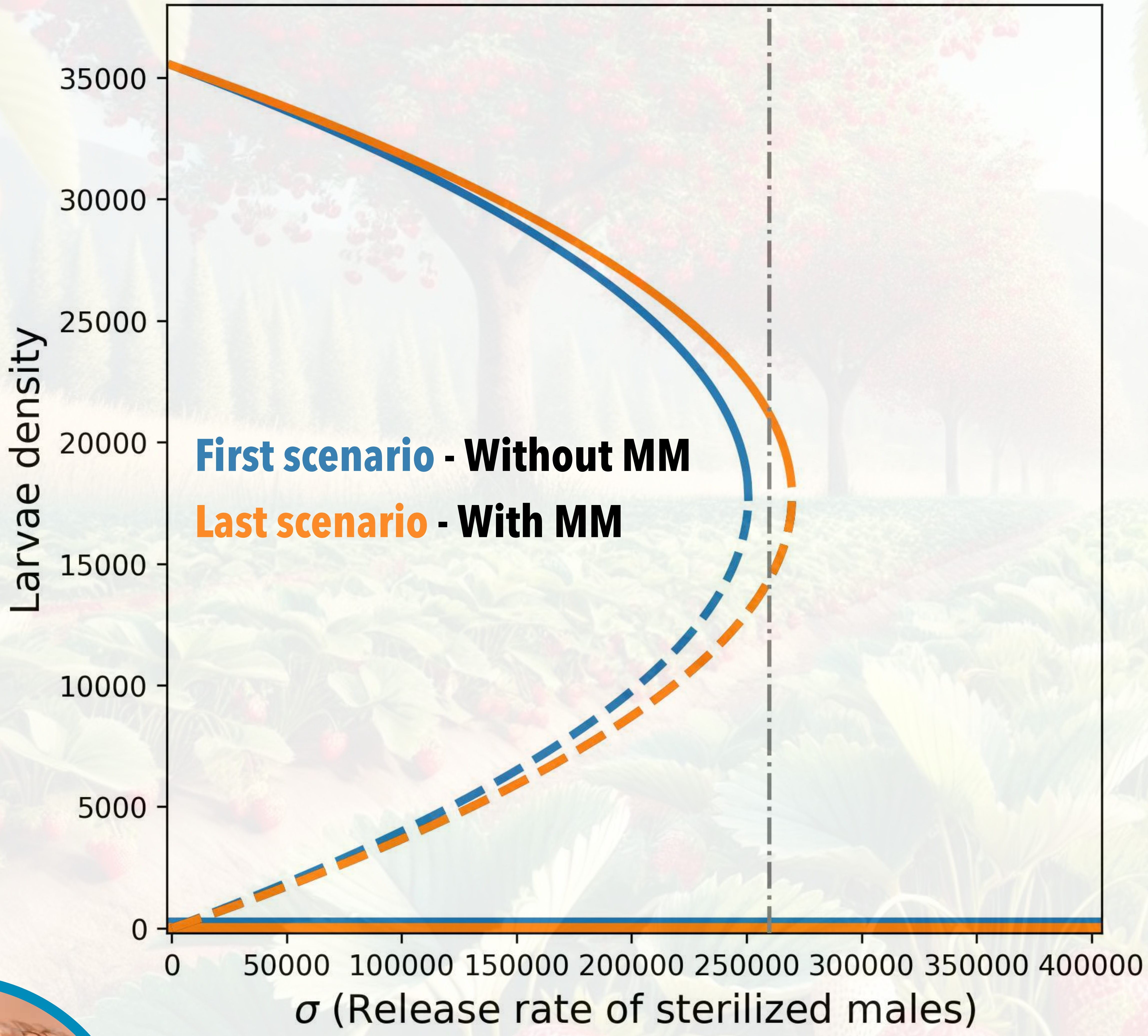

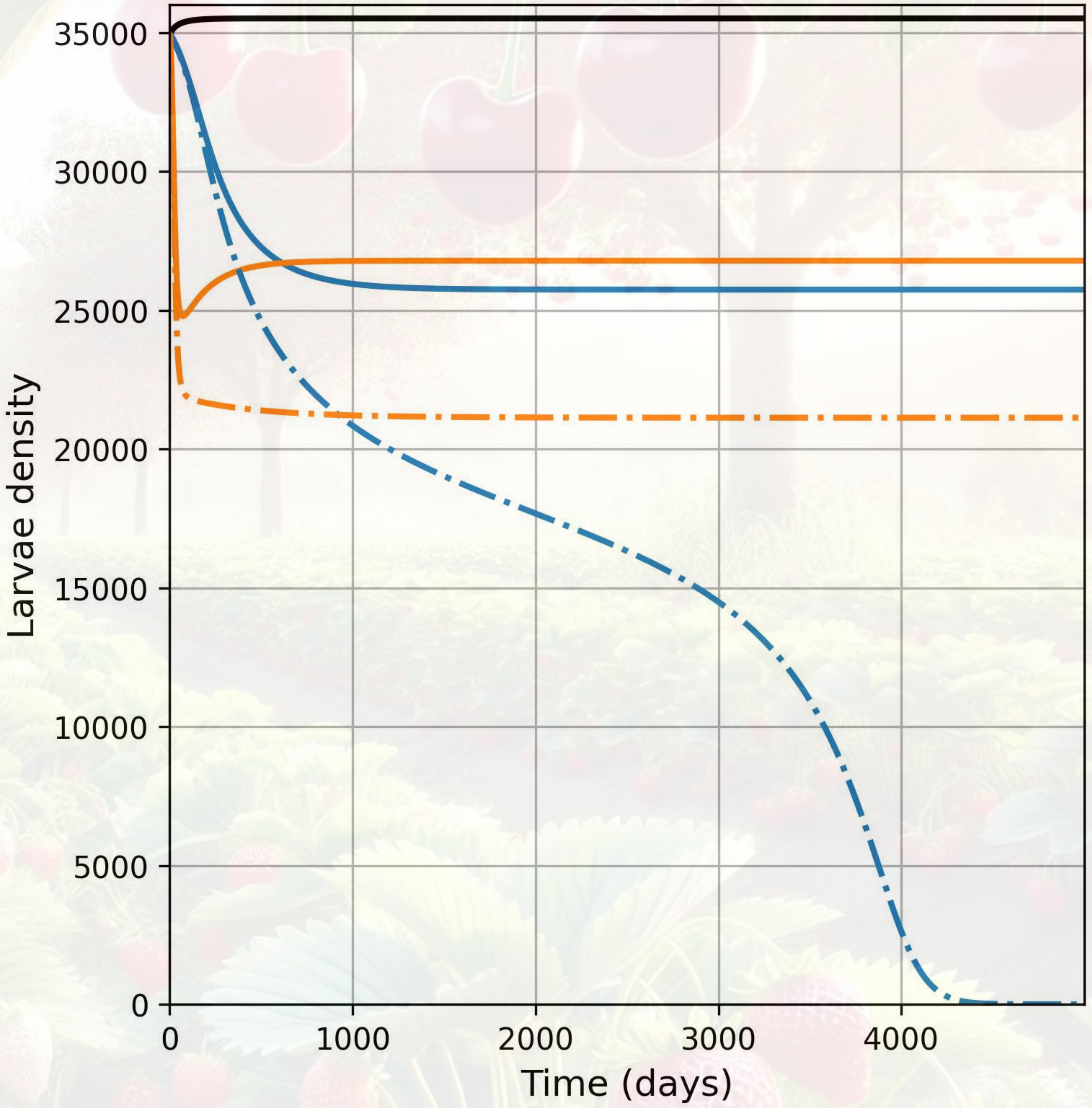

Drosophila suzukii

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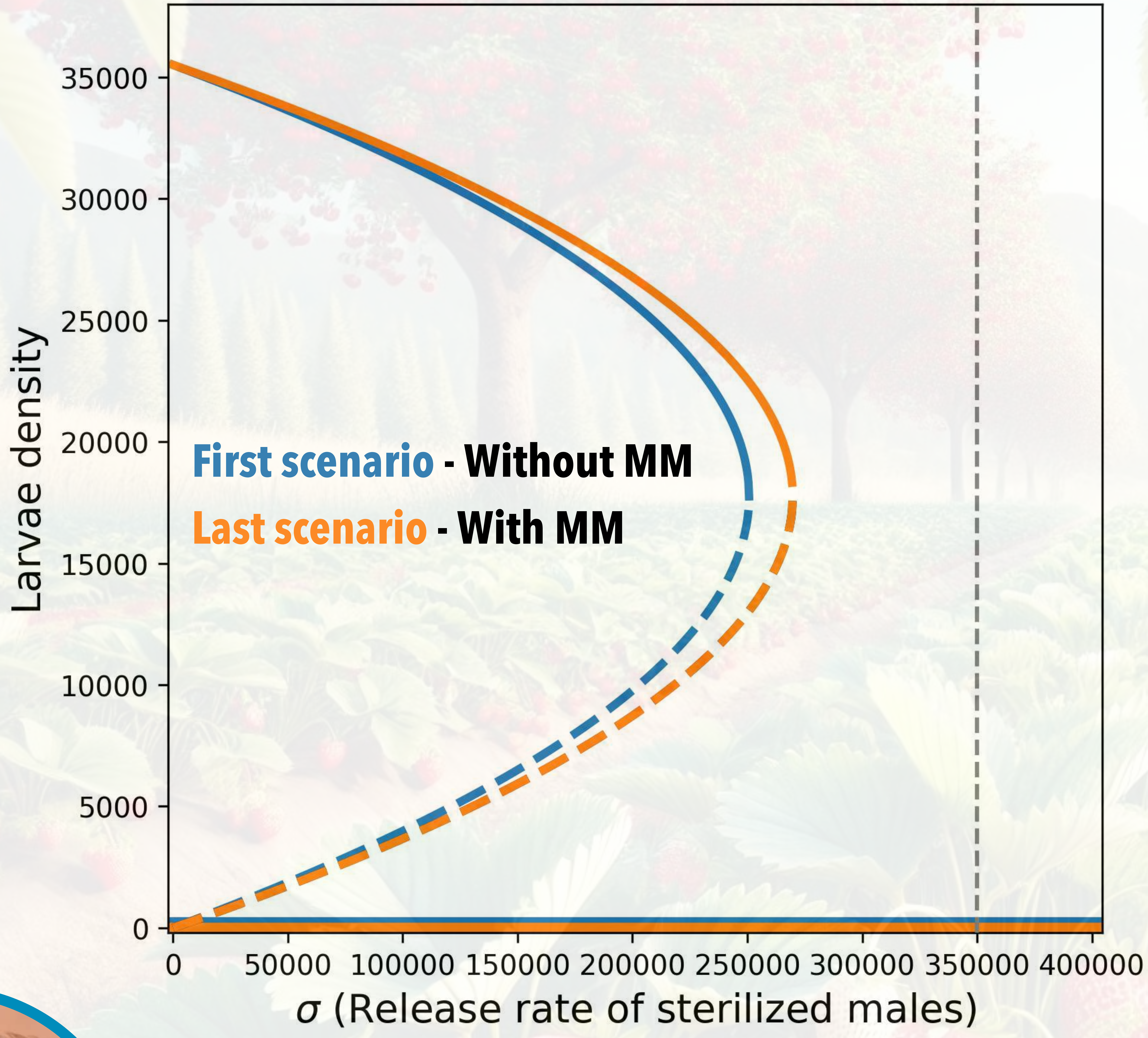

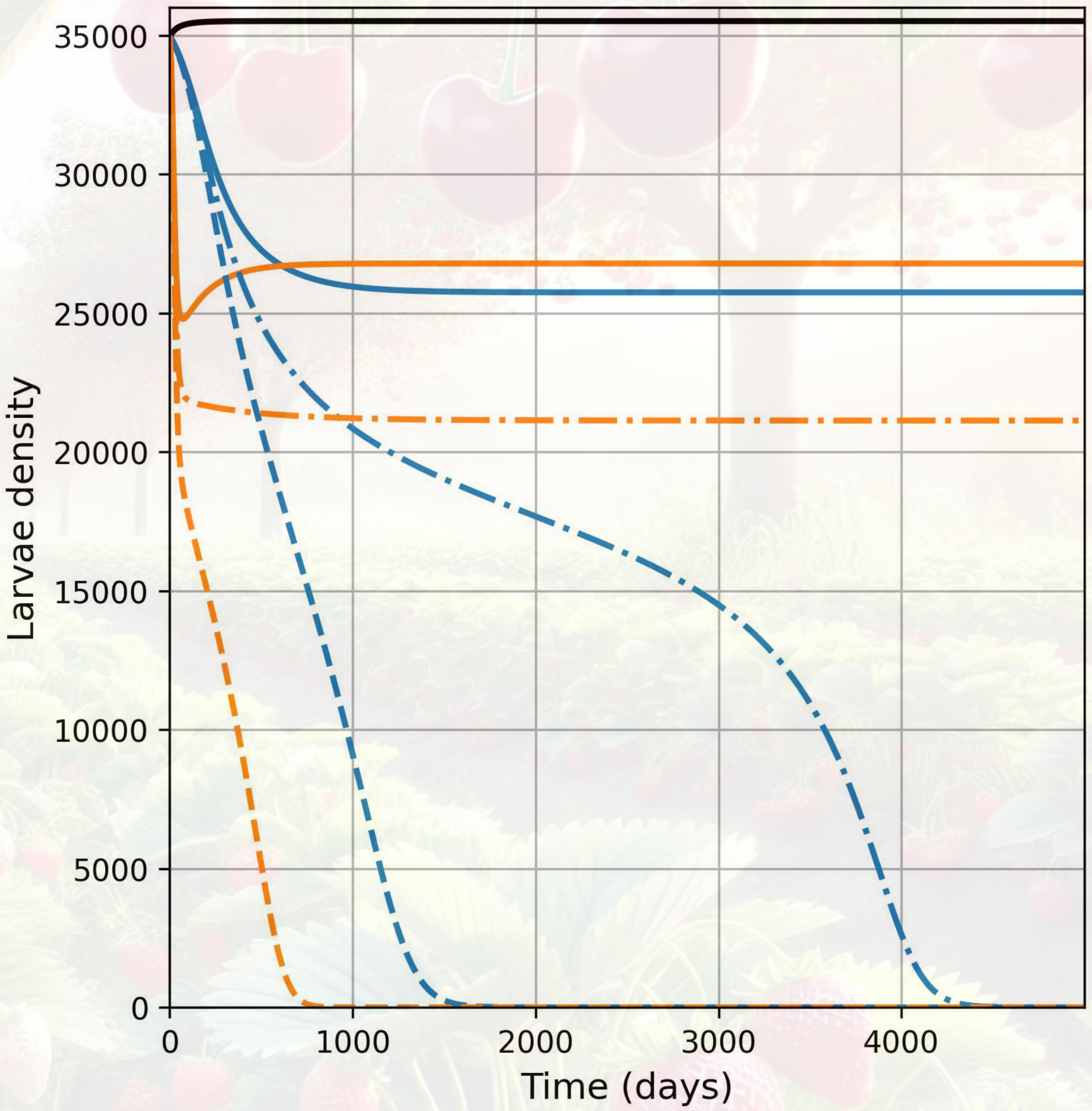

Drosophila suzukii

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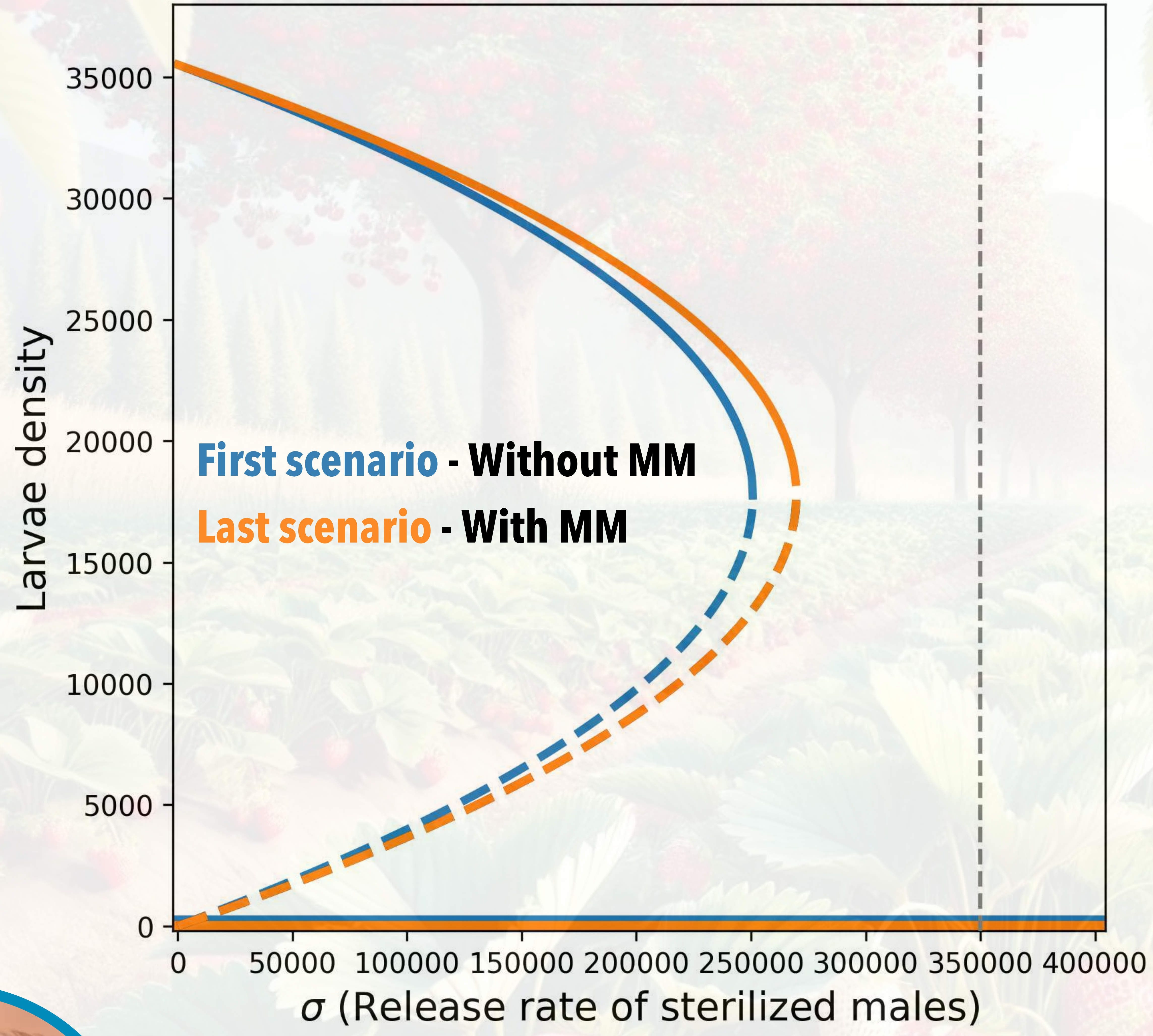

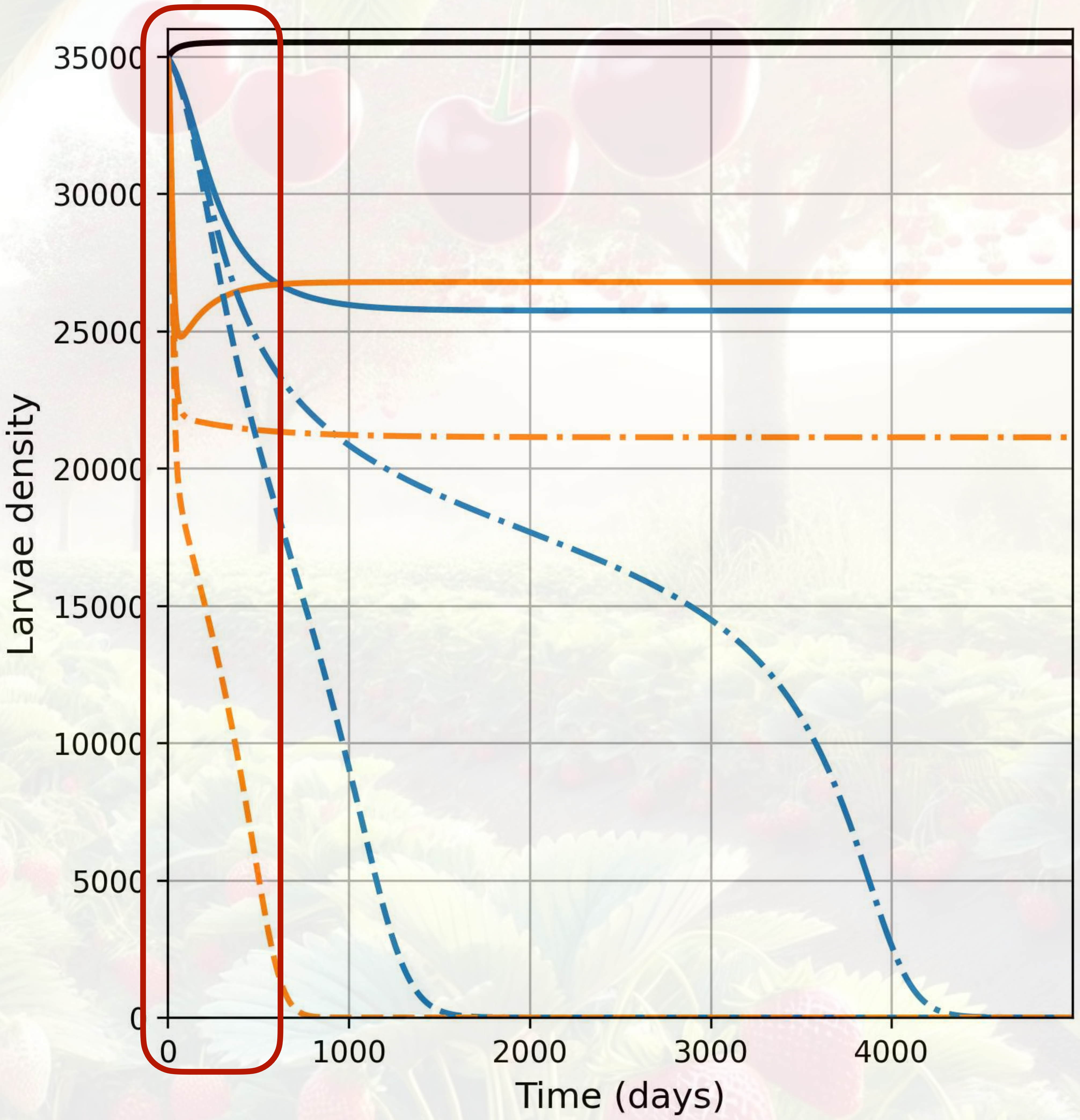

Drosophila suzukii

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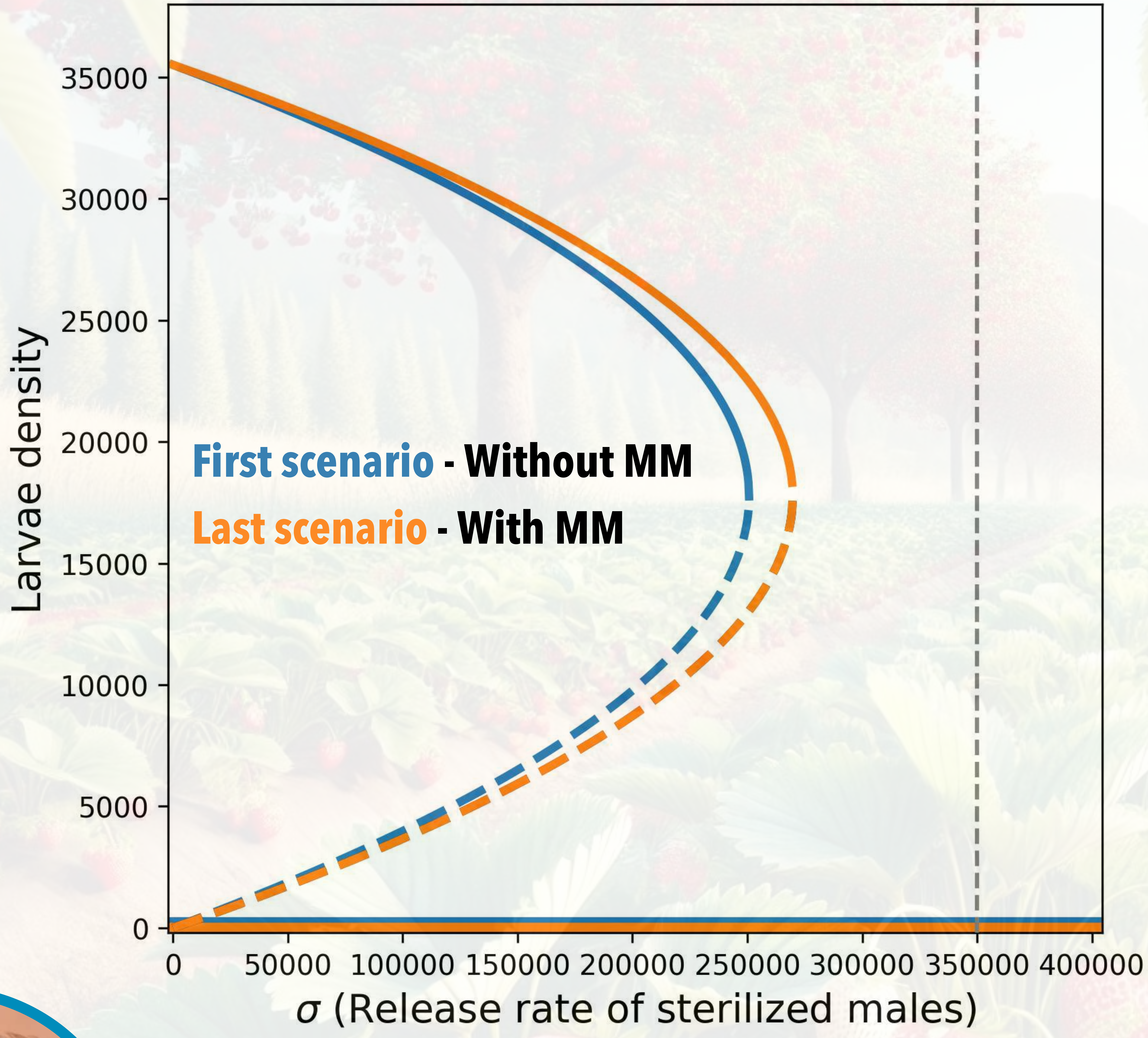
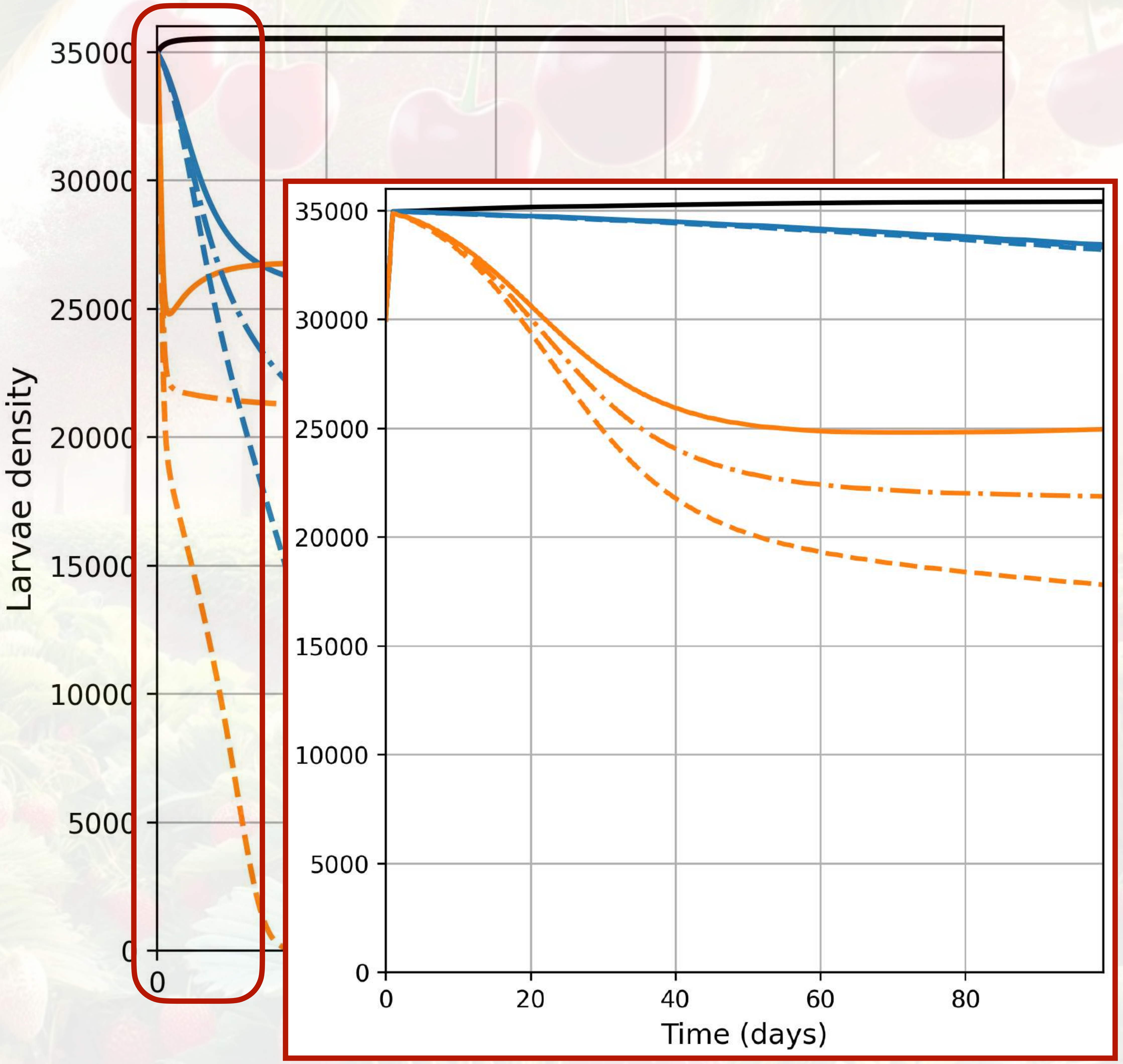
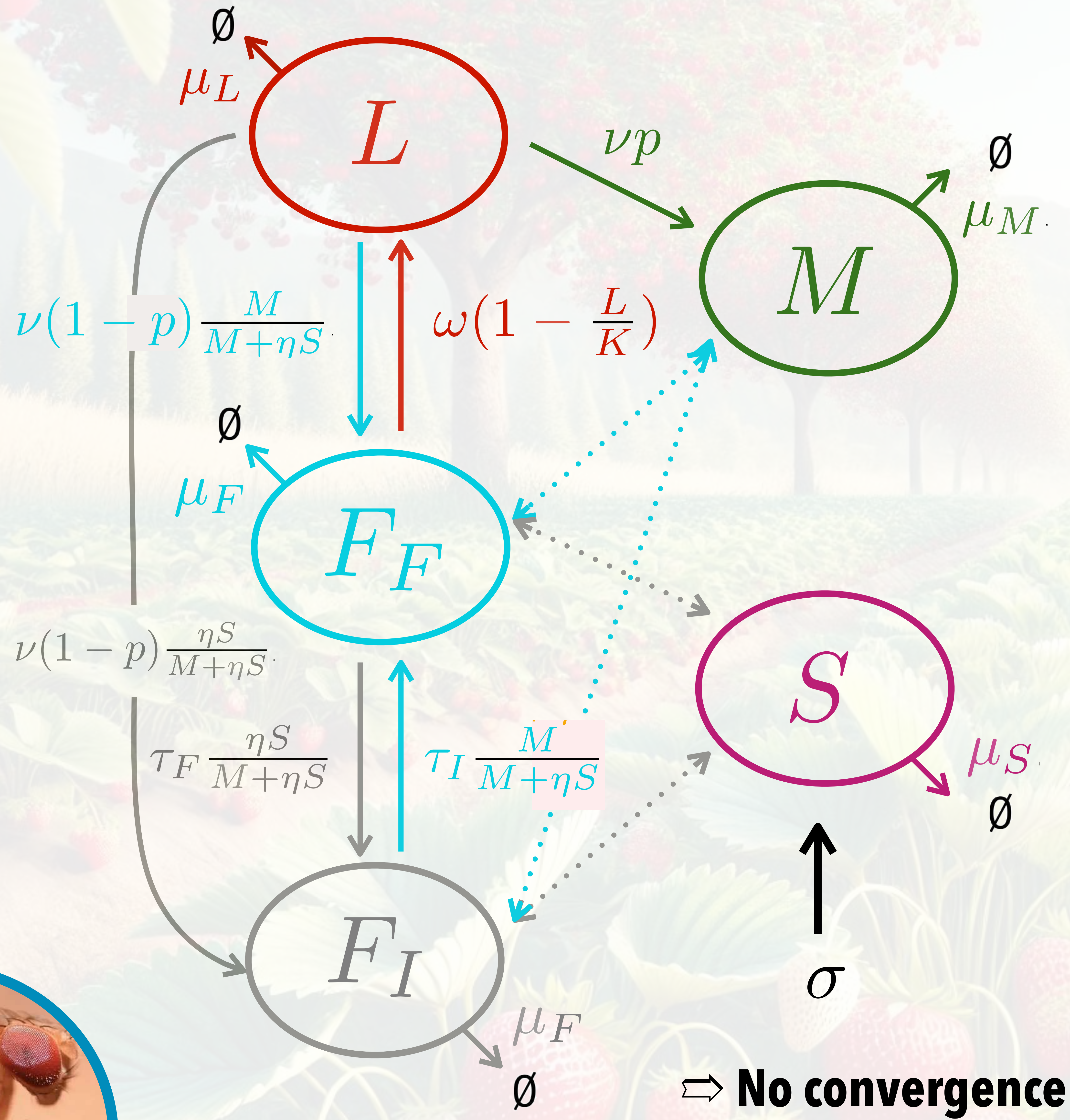


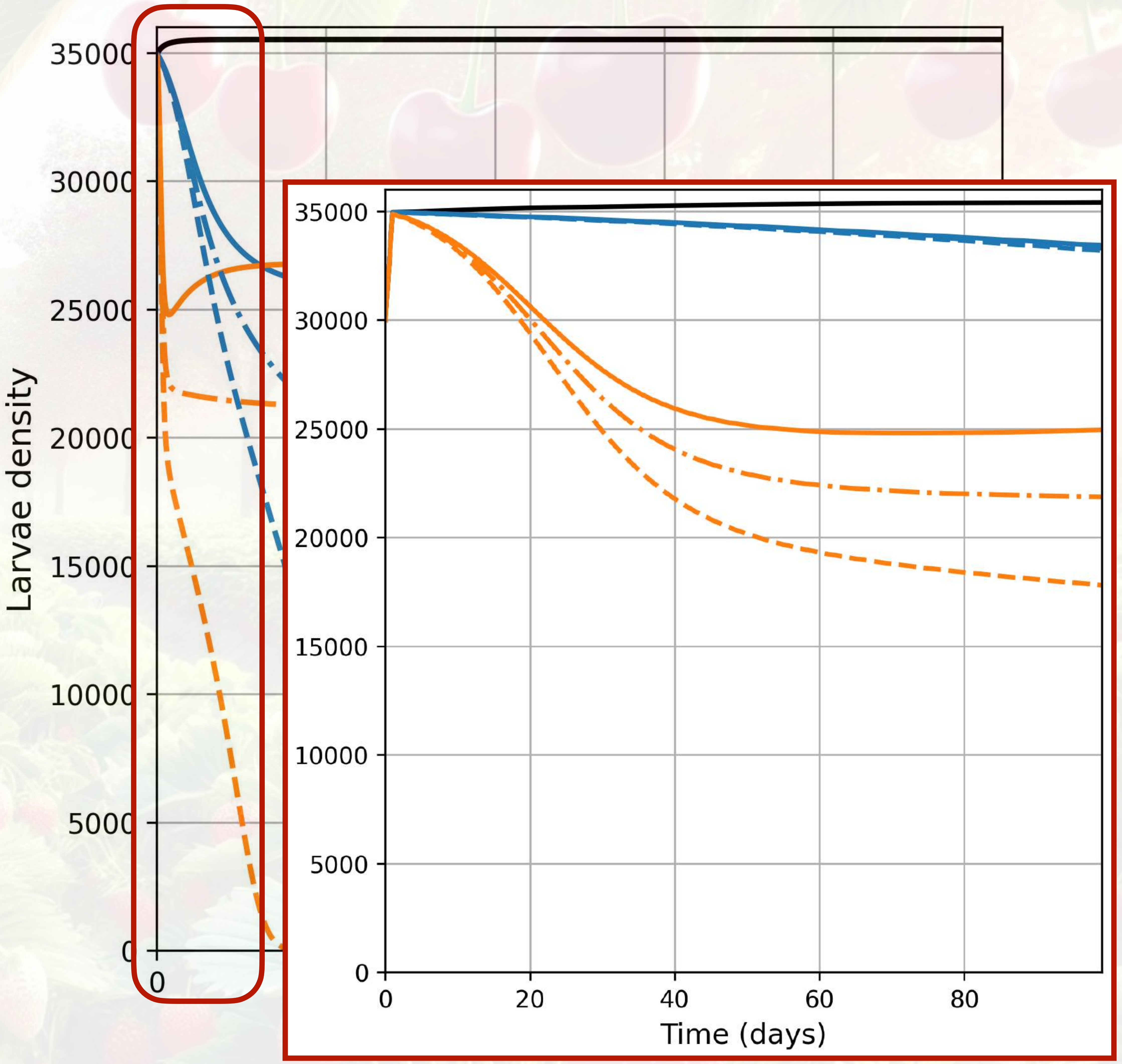


⇨ **No convergence between transient dynamics and long-term equilibrium**

Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate





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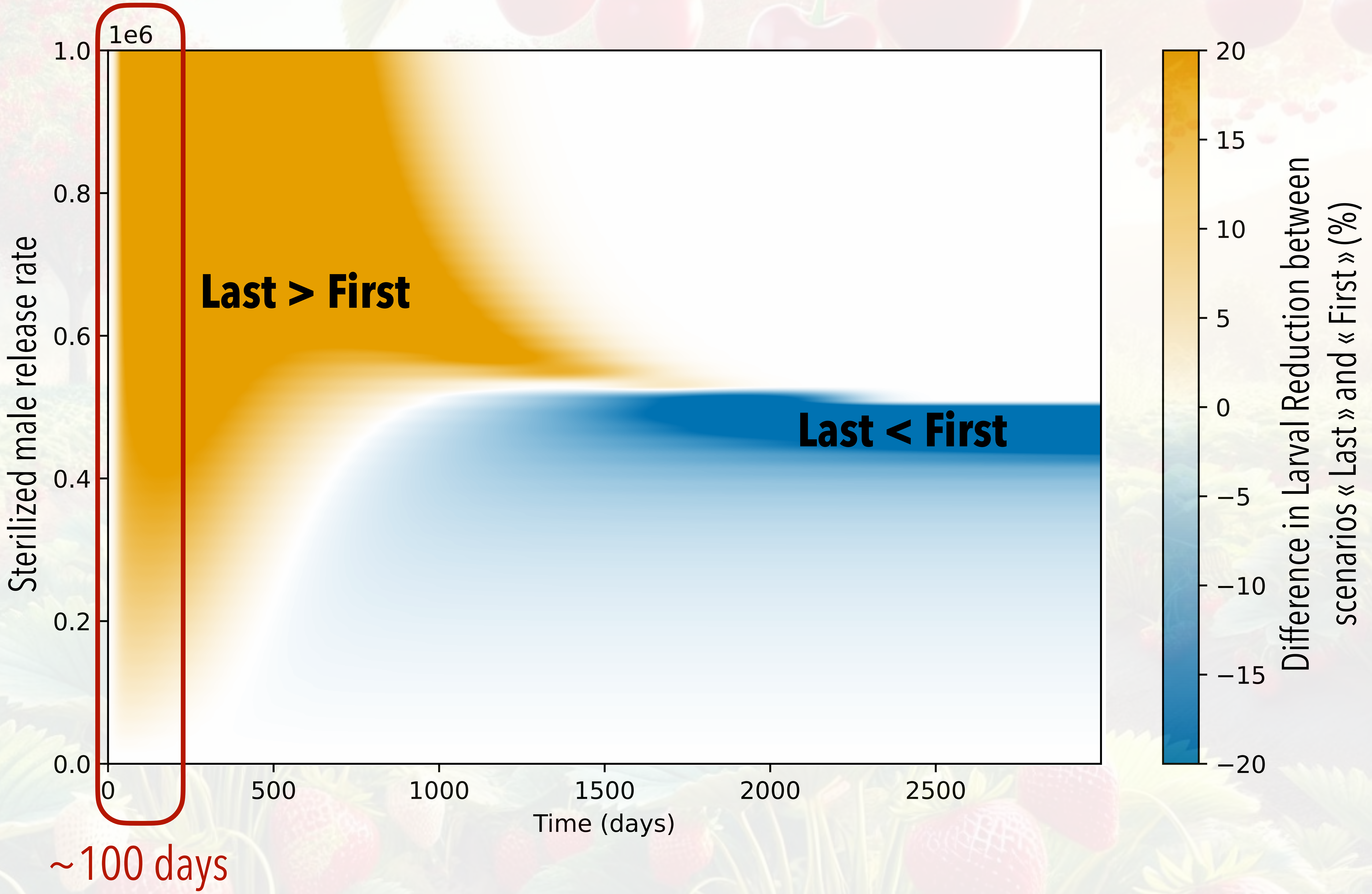
Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

- With MM = Use of Last sperm
- Without MM = Use of First sperm
- « **>** » = better reduction



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Drosophila suzukii

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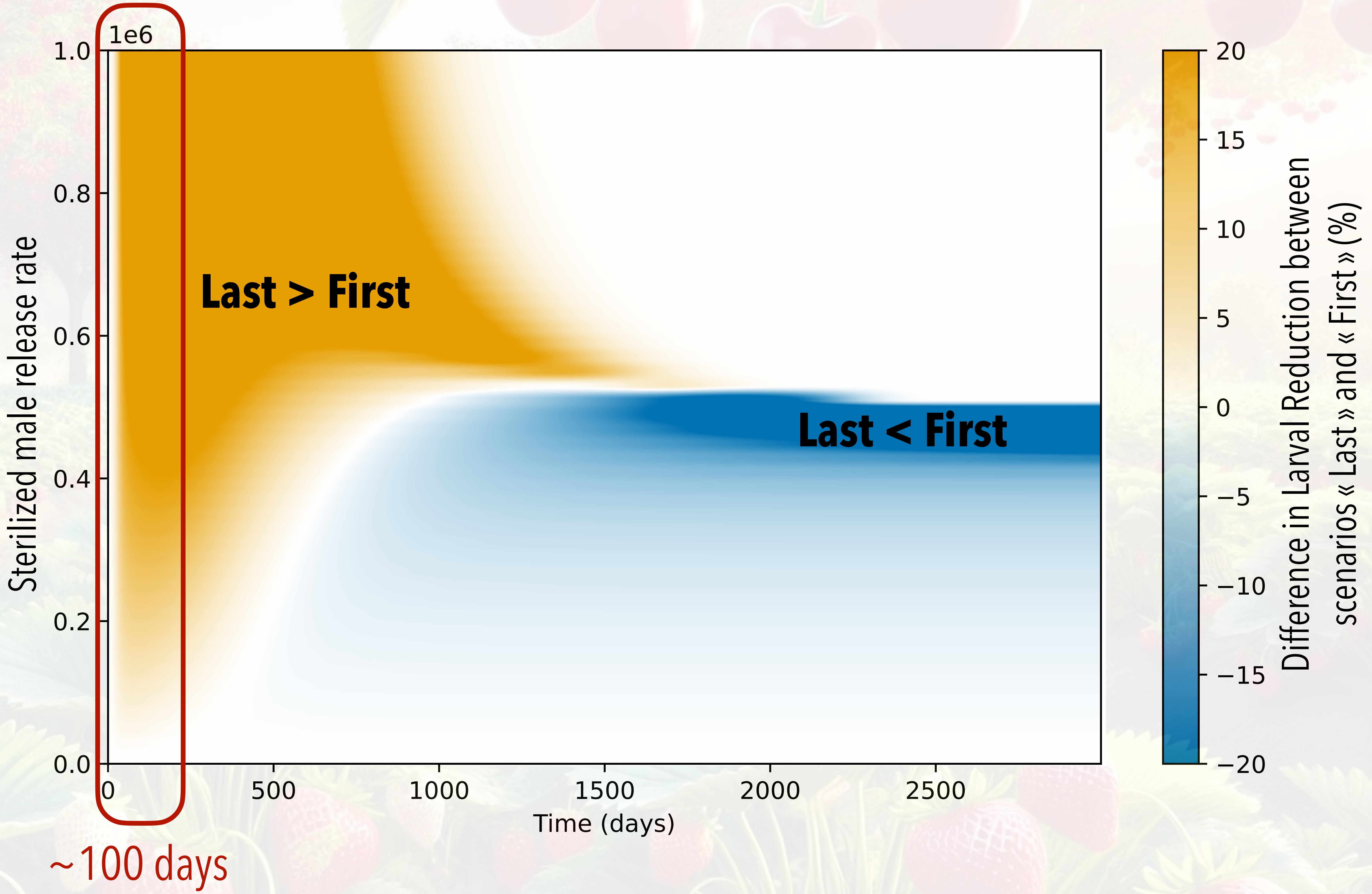
➪ MM is not incompatible with SIT; it can even be beneficial over a short season by accelerating female « defertilization » through re-mating with sterilized males



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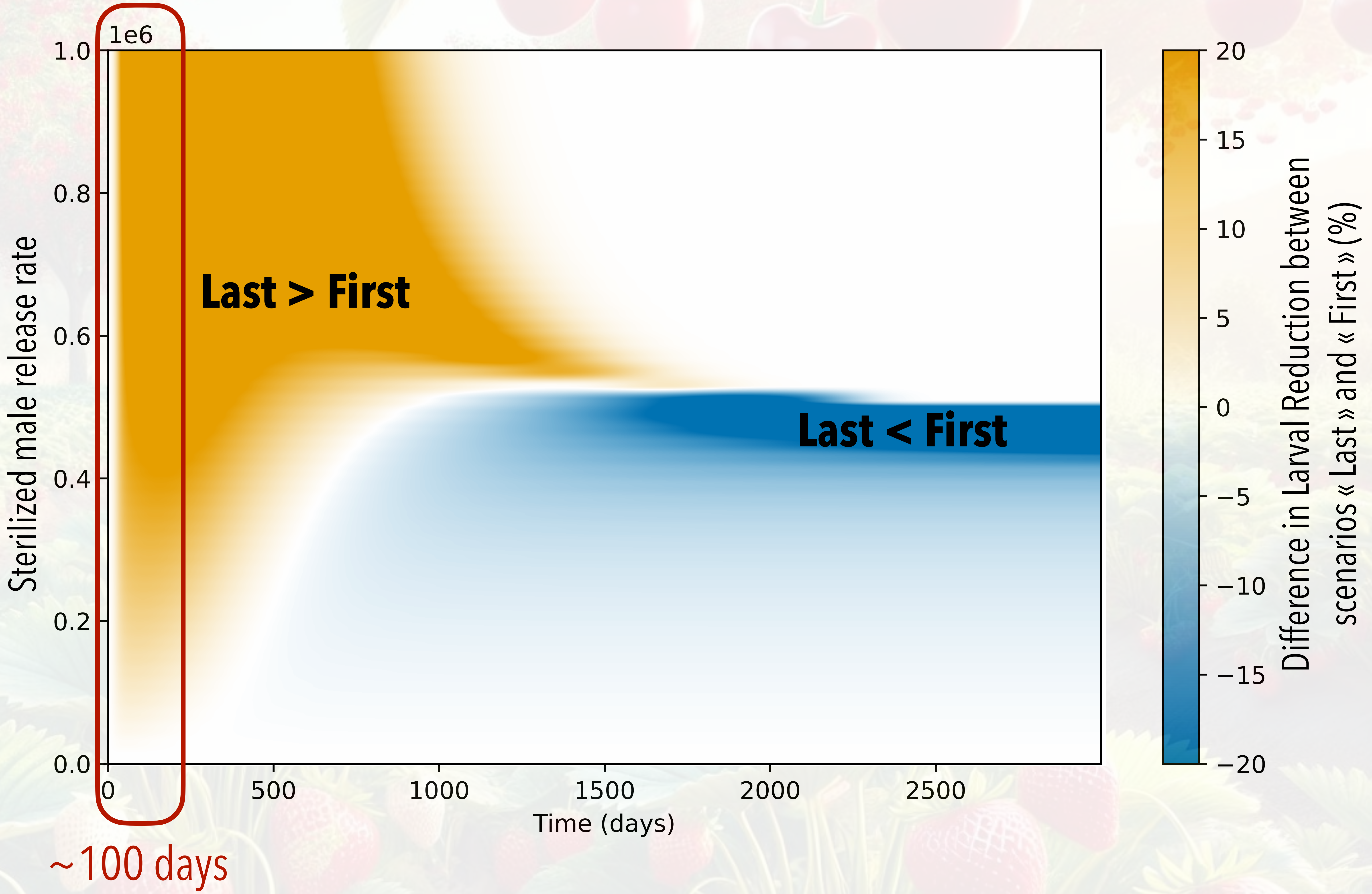


➯ **No convergence between transient dynamics and long-term equilibrium**

What about more complex sperm use biases?

Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

- **No data** on the use of sperm in *D.suzukii*…

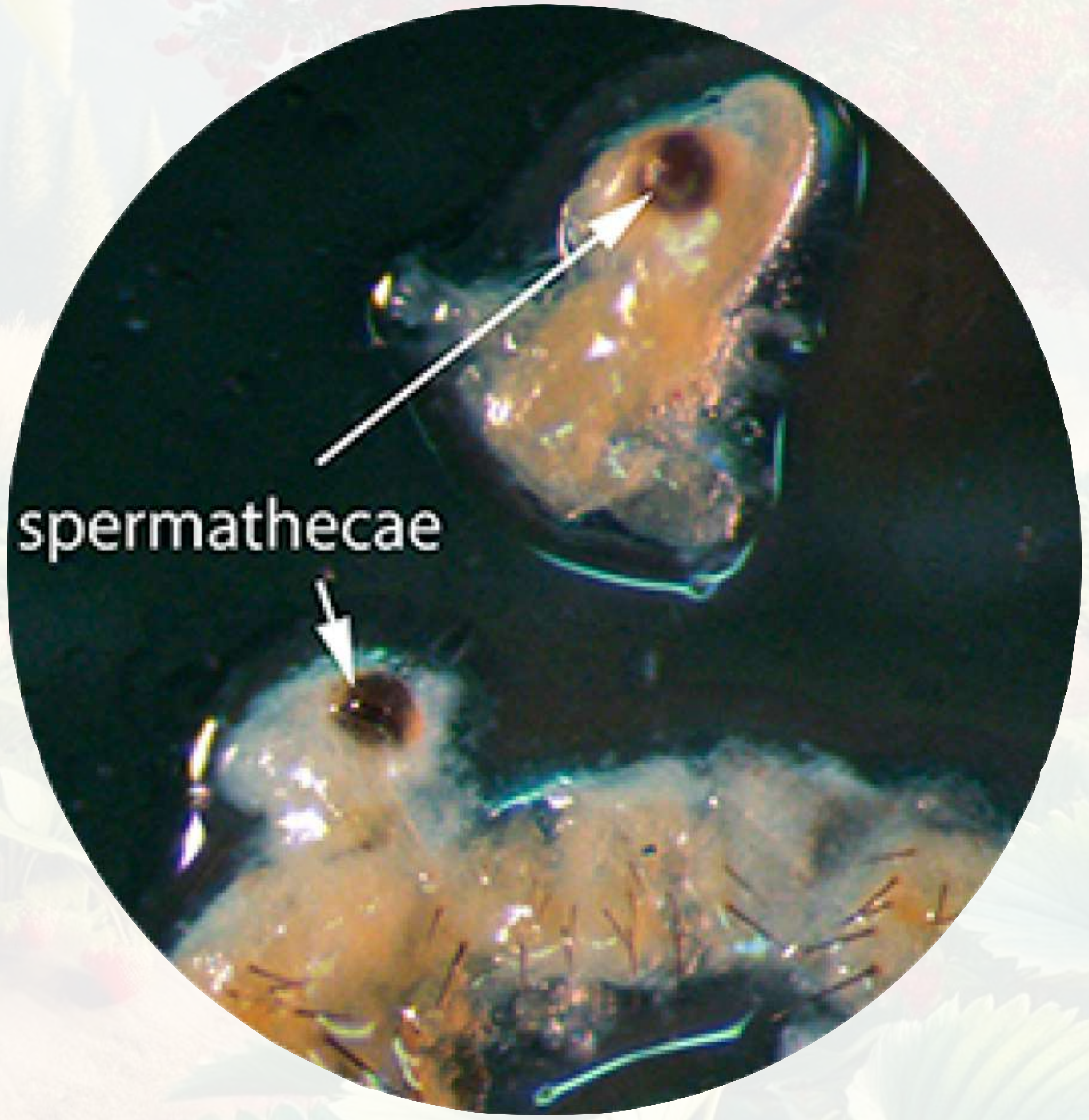
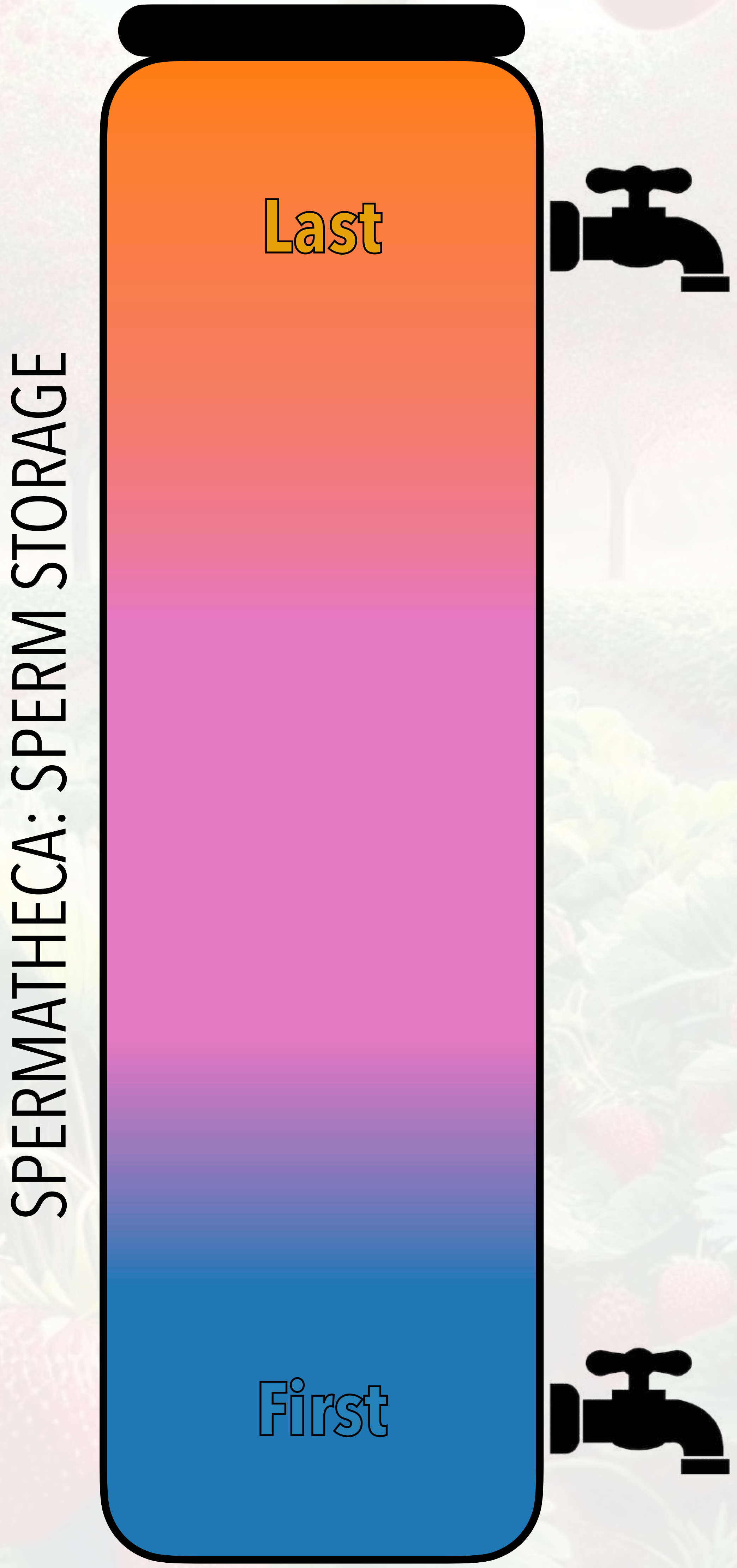


Fig. extracted from Avanesyan et al. 2017



➪ 2 spermathecae (Avanesyan et al. 2017)

➪ Offspring from ~2-5 males (Puppato et al, 2023)

➪ First-male parentage preference (Chen et al, 2022)

Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

- **No data** on the use of sperm in *D.suzukii*…

…but data for *D.melanogaster* and *D.hibisci*

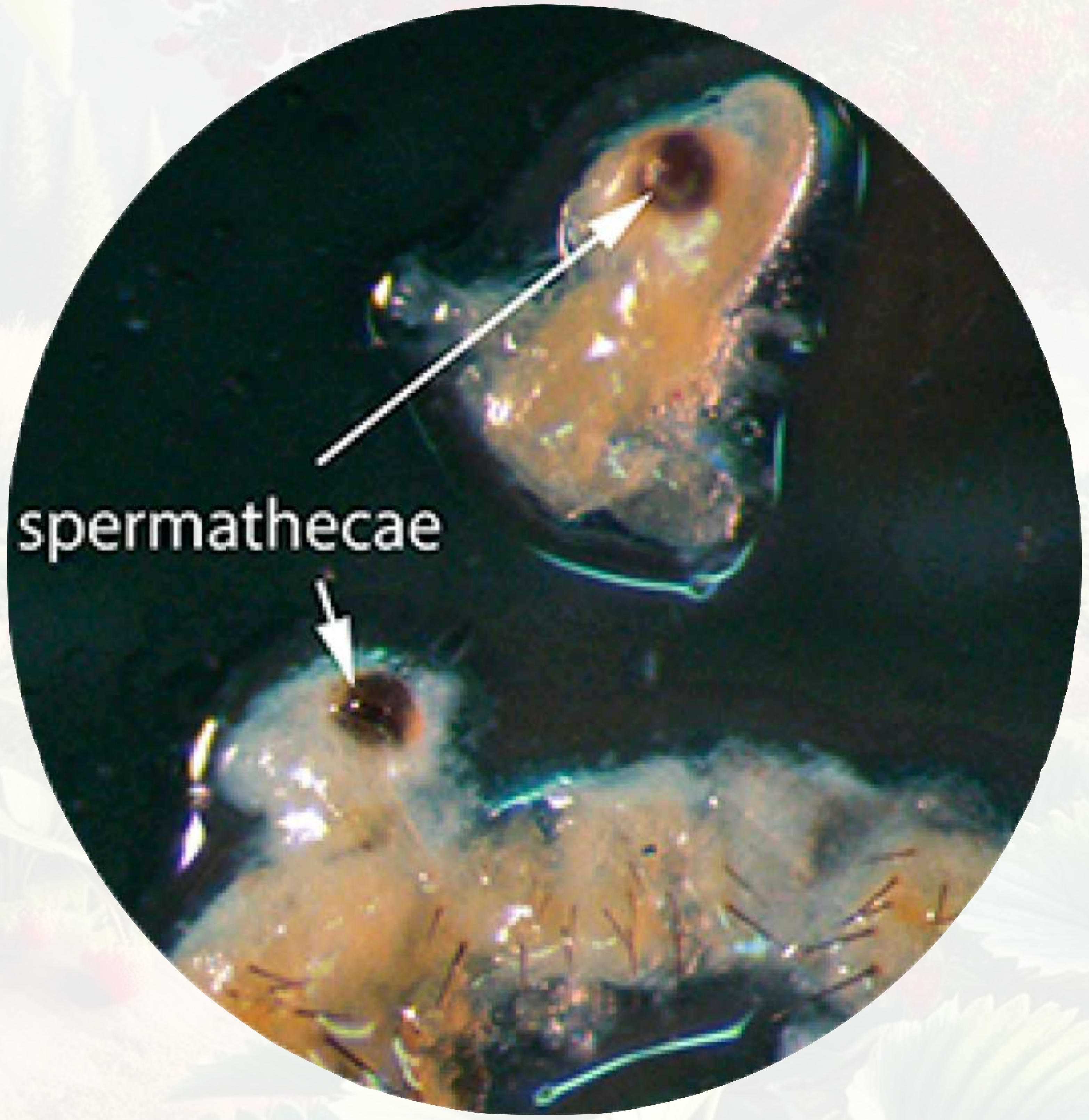


Fig. extracted from Avanesyan et al. 2017

SPERMATHECA: SPERM STORAGE

➪ Production of > 80% offspring (Qazi et al, 2003)

➪ Storage of sperm from > 2 males simultaneously (Bangham et al, 2003)

➪ 2 spermathecae (Avanesyan et al. 2017)

➪ Offspring from ~2-5 males (Puppato et al, 2023)

➪ Existence of mating plug (Polak et al. 2001)

➪ ⇲ storage of 2nd sperm (Hopkins et al, 2020)

➪ First-male parentage preference (Chen et al, 2022)

Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

Die?
time ≧ death_date?
Y
Agent deleted

Die?
time ≧ death_date?
Y
Agent deleted

N
Die?
Y → Agent deleted
N
Emerging?
time ≧ emergence_date?
Y
Agent deleted
Female?
Binomial distribution, p=0.5
Y → Female creation
N → Male creation

Die?
time ≧ death_date?
Y → Agent deleted
N
Available to mate?
time_until_next_mating = 0?
N → time_until_next_mating –= 1
Y

Mating
- **Partner selection:** Bernoulli distribution, p = proportion of wild males
- **Update the spermatheca**
- **Update time:** time_until_next_mating = refractory period

Use of sperm from the spermatheca
« First », «Last», « Mixed »,
« Preference W»,
« Preference I»,
« Preference S»

Use of fertile sperm?
Y
Larvae creation

⇨ Development of an **agent-based model** to explore how potential **sperm use biases** impact pest control with SIT

Drosophila suzukii

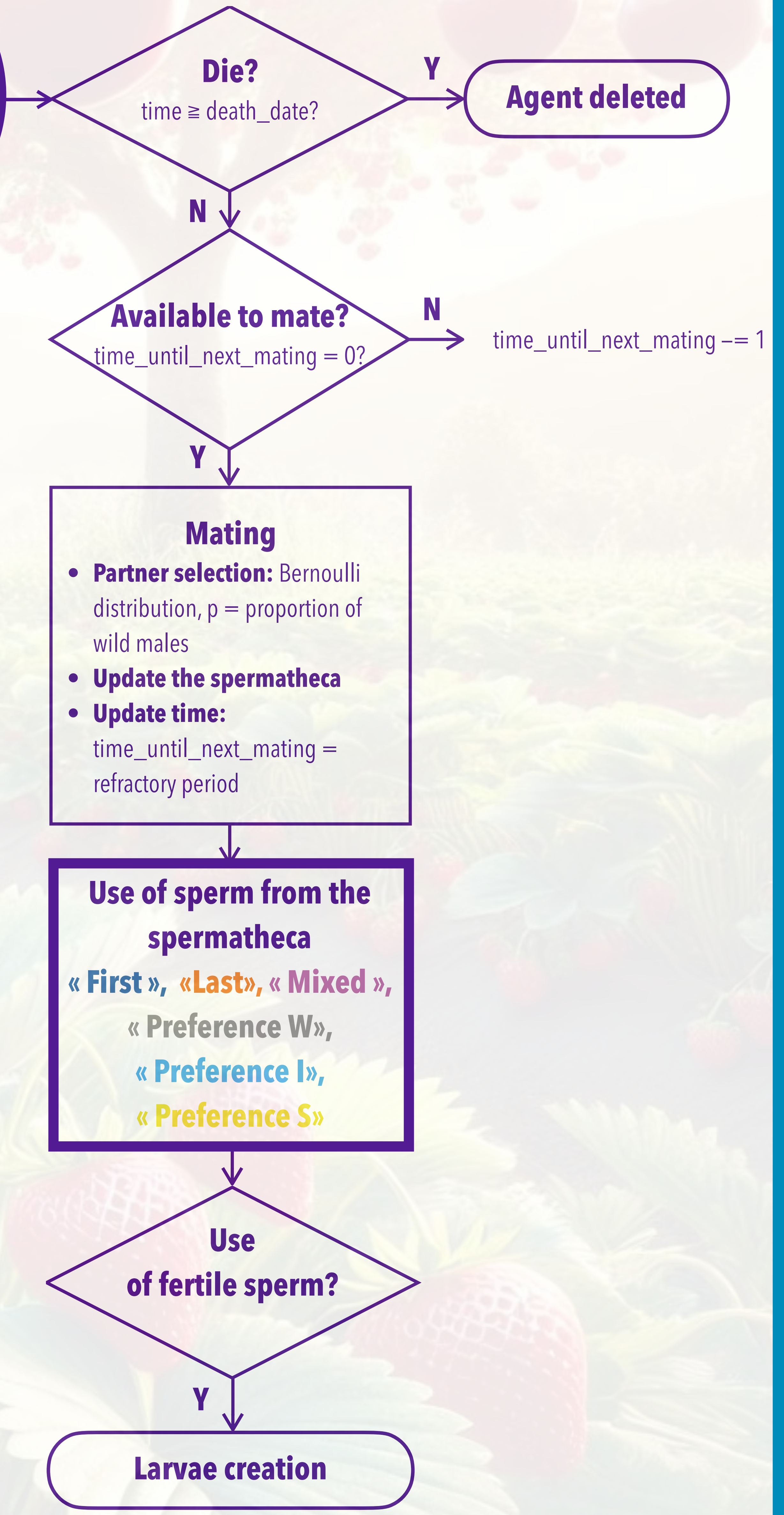
(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?




SPERM USE BIASES

- **« First »:** Females use sperm from their first mating
- **« Last »:** Females use sperm from their last mating
- **« Mixed »:** No preference (Egg-laying is proportional to the fertile sperm content of the spermatheca)
- **« Preference W »:** 100% preference for fertile sperm
- **« Preference I »:** 80% preference for fertile sperm (biological data)
- **« Preference S »:** 100% preference for sterile sperm



Drosophila suzukii

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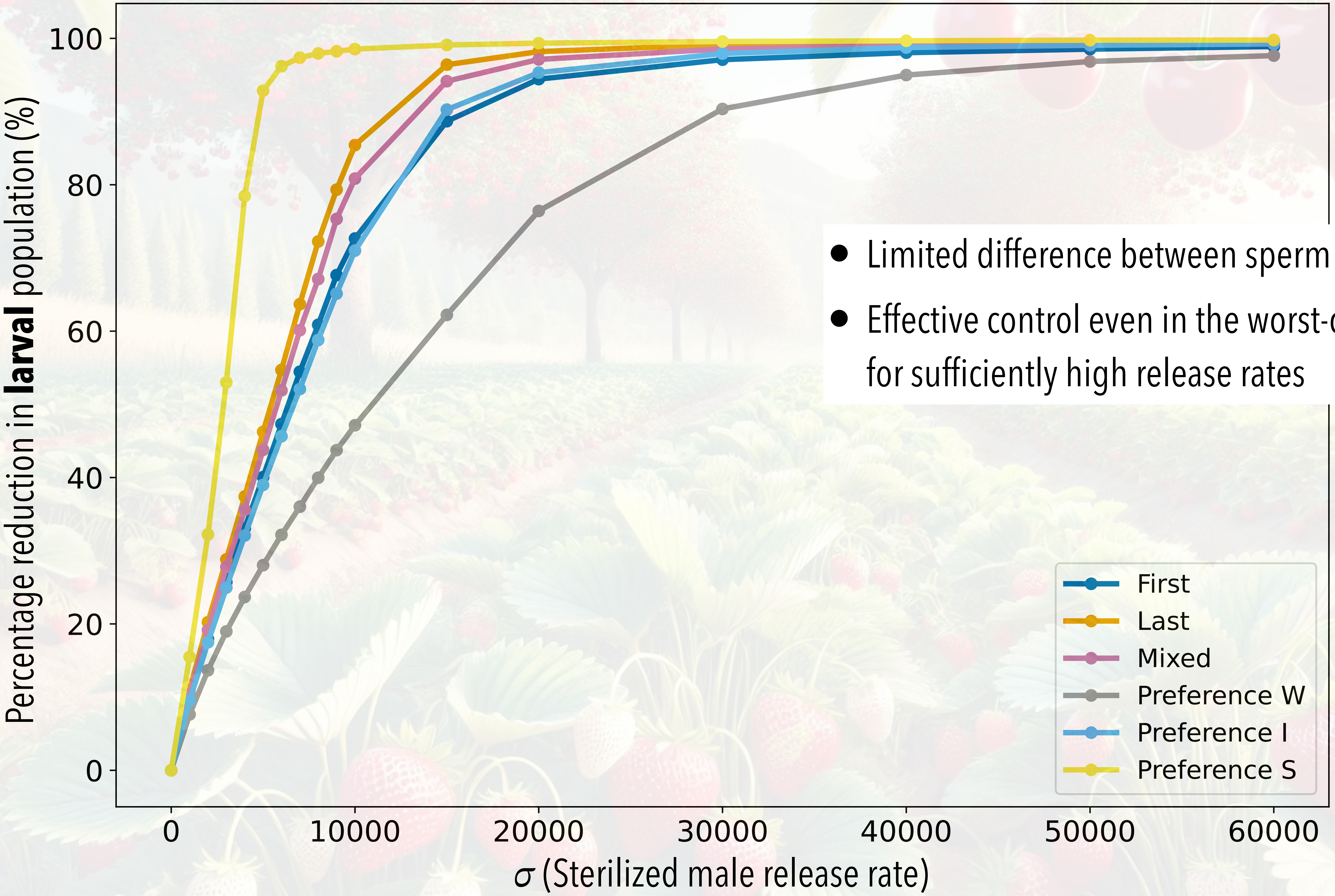


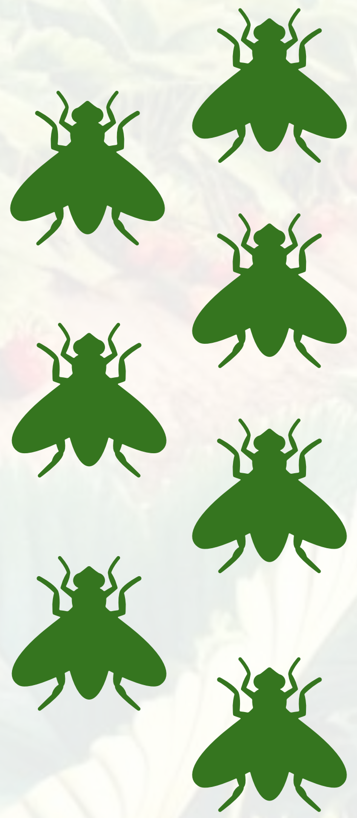
- Limited difference between sperm use biases
- Effective control even in the worst-case scenario for sufficiently high release rates

Discussion - Conclusion

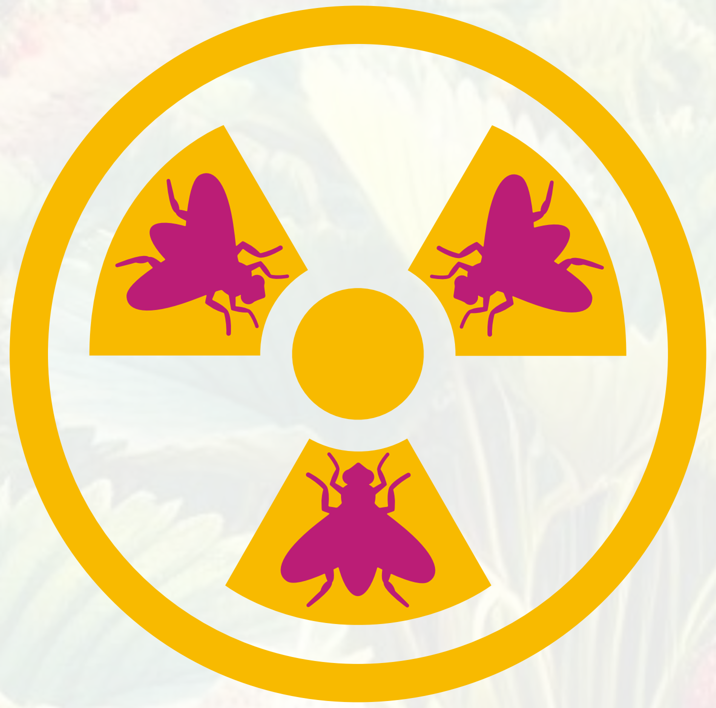
Take home message

PRODUCTION | **SEXING** | **STERILIZATION** | **MASS RELEASES** | **DILUTION OF WILD POPULATIONS**

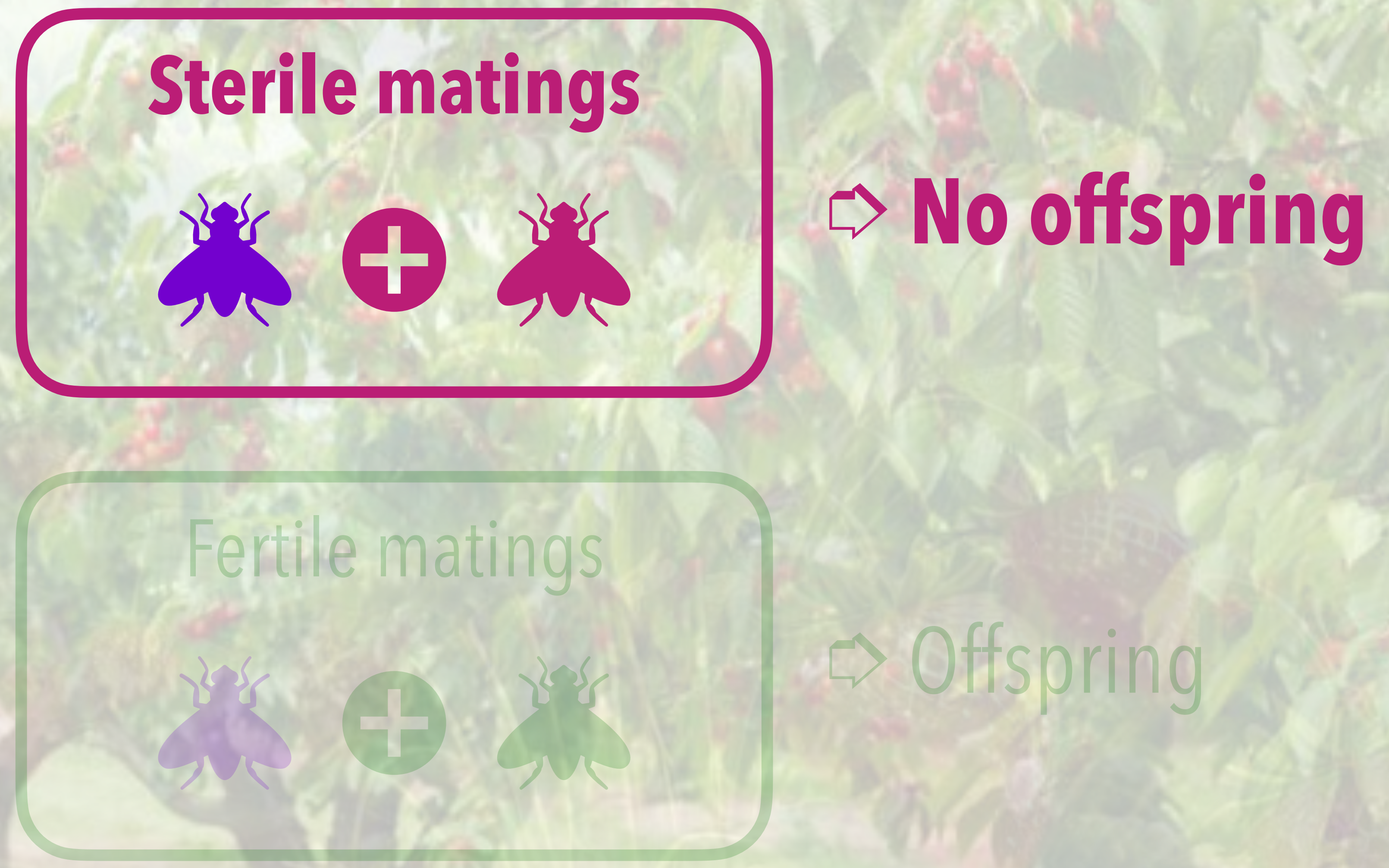
Mass-rearing of targeted insects



Separation to keep only males



Exposure to ionizing radiation

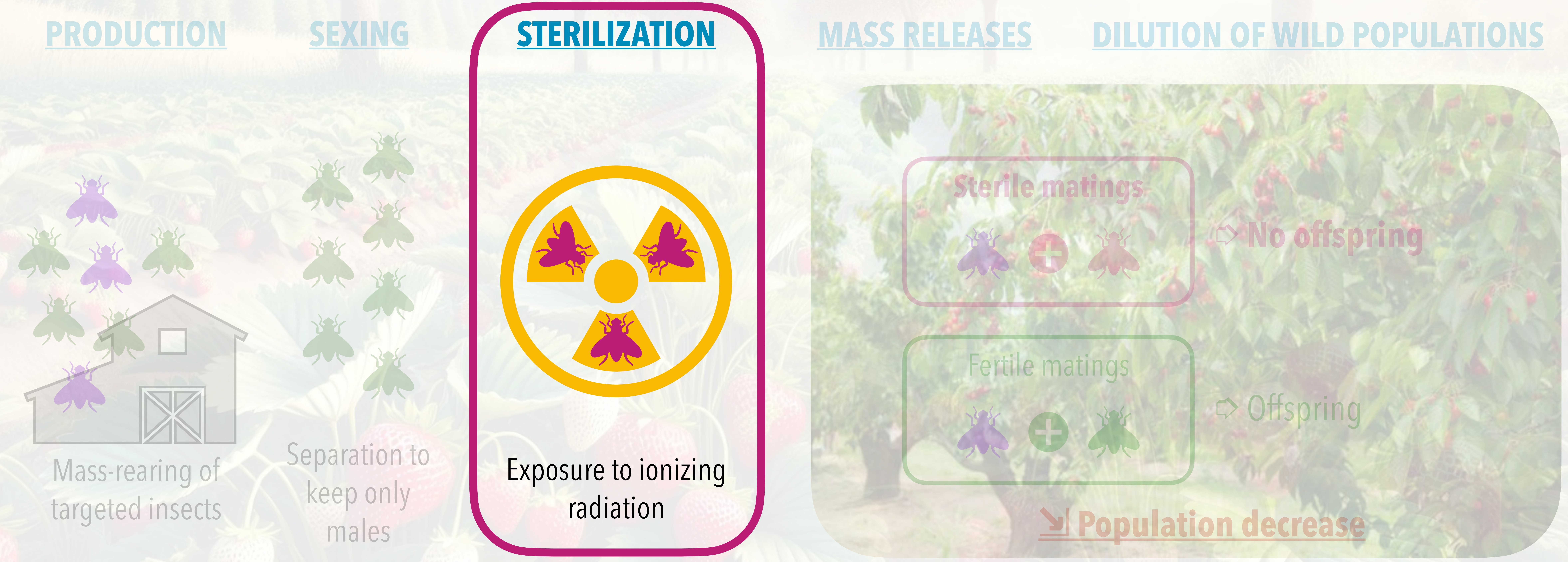


↘ Population decrease

Take home message

Technical constraint: Residual Fertility

- **Strong** impact of **residual fertility** on SIT efficiency
- A certain level of residual fertility **can be tolerated** as long as the **fertile irradiated males are just as bad as the sterile irradiated males.**



Take home message

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Biological constraint: Multiple Matings

- **Not incompatible** with SIT… **can even be beneficial!**
- **Varied** impact of **multiple mating** depending on bias and release rate

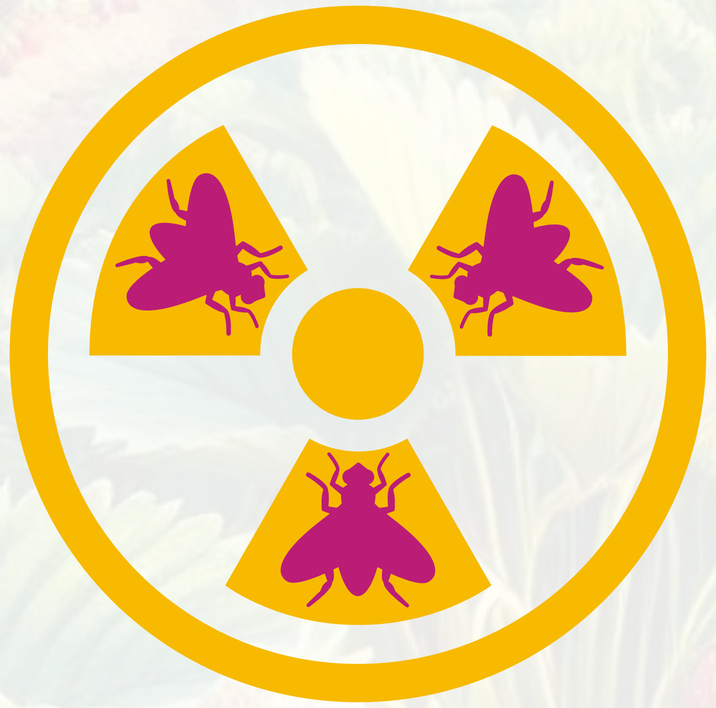
PRODUCTION

Mass-rearing of targeted insects

SEXING

Separation to keep only males

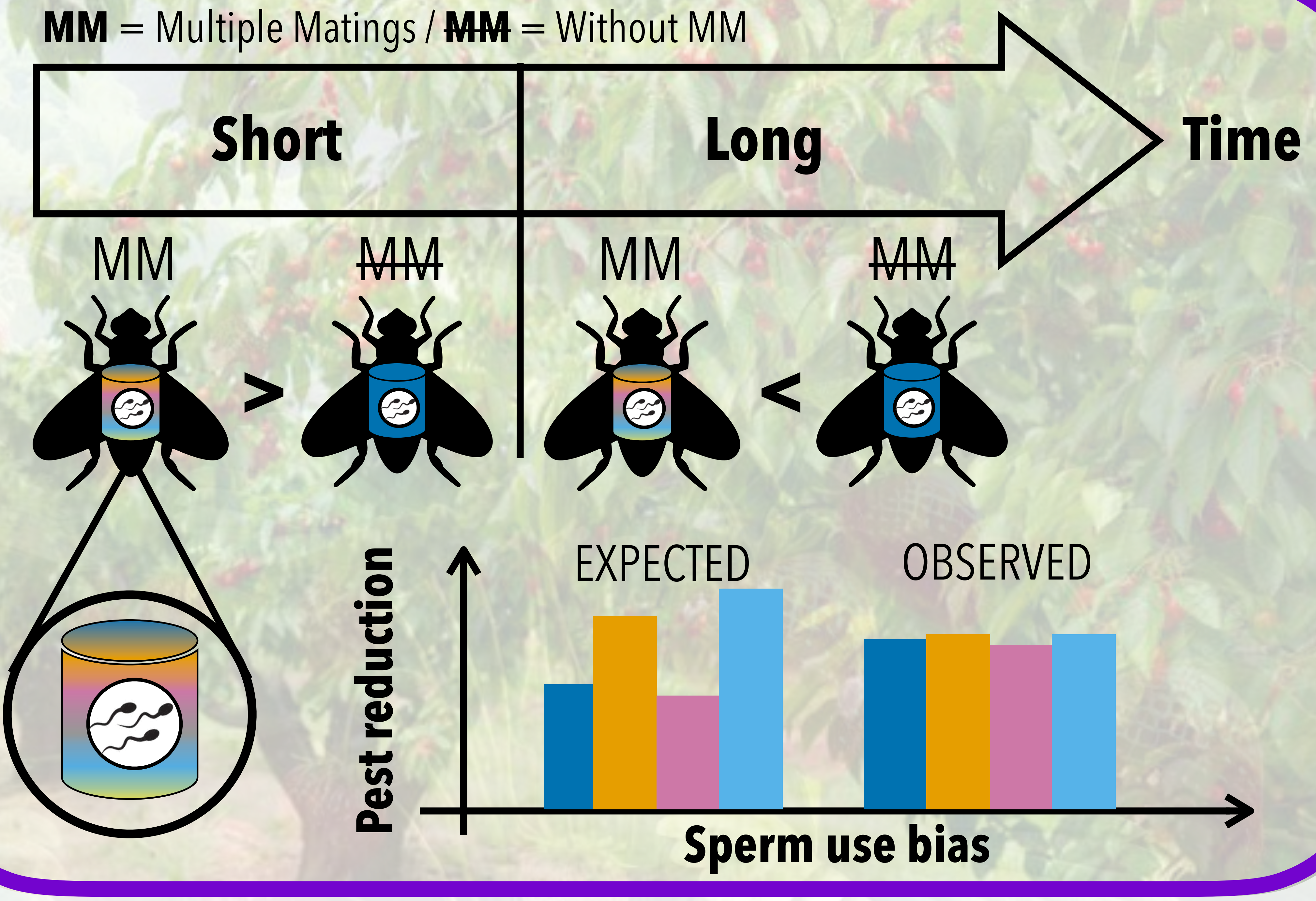
STERILIZATION



Exposure to ionizing radiation

MASS RELEASES

DILUTION OF WILD POPULATIONS



Take home message

The competitiveness of sterilized males remains a key leverage point.

Technical constraint: Residual Fertility

- **Strong** impact of **residual fertility** on SIT efficiency
- A certain level of residual fertility **can be tolerated** as long as the **fertile irradiated males are just as bad as the sterile irradiated males.**

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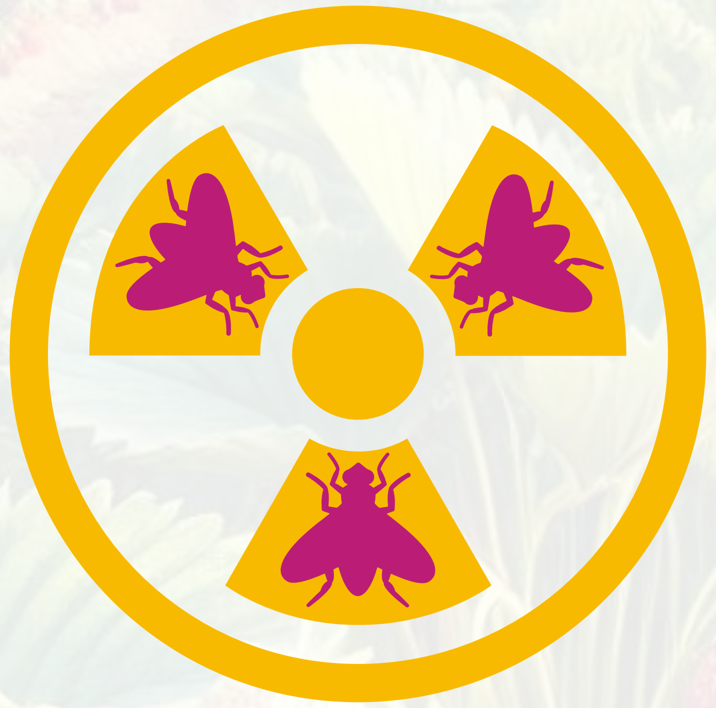
PRODUCTION

Mass-rearing of targeted insects

SEXING

Separation to keep only males

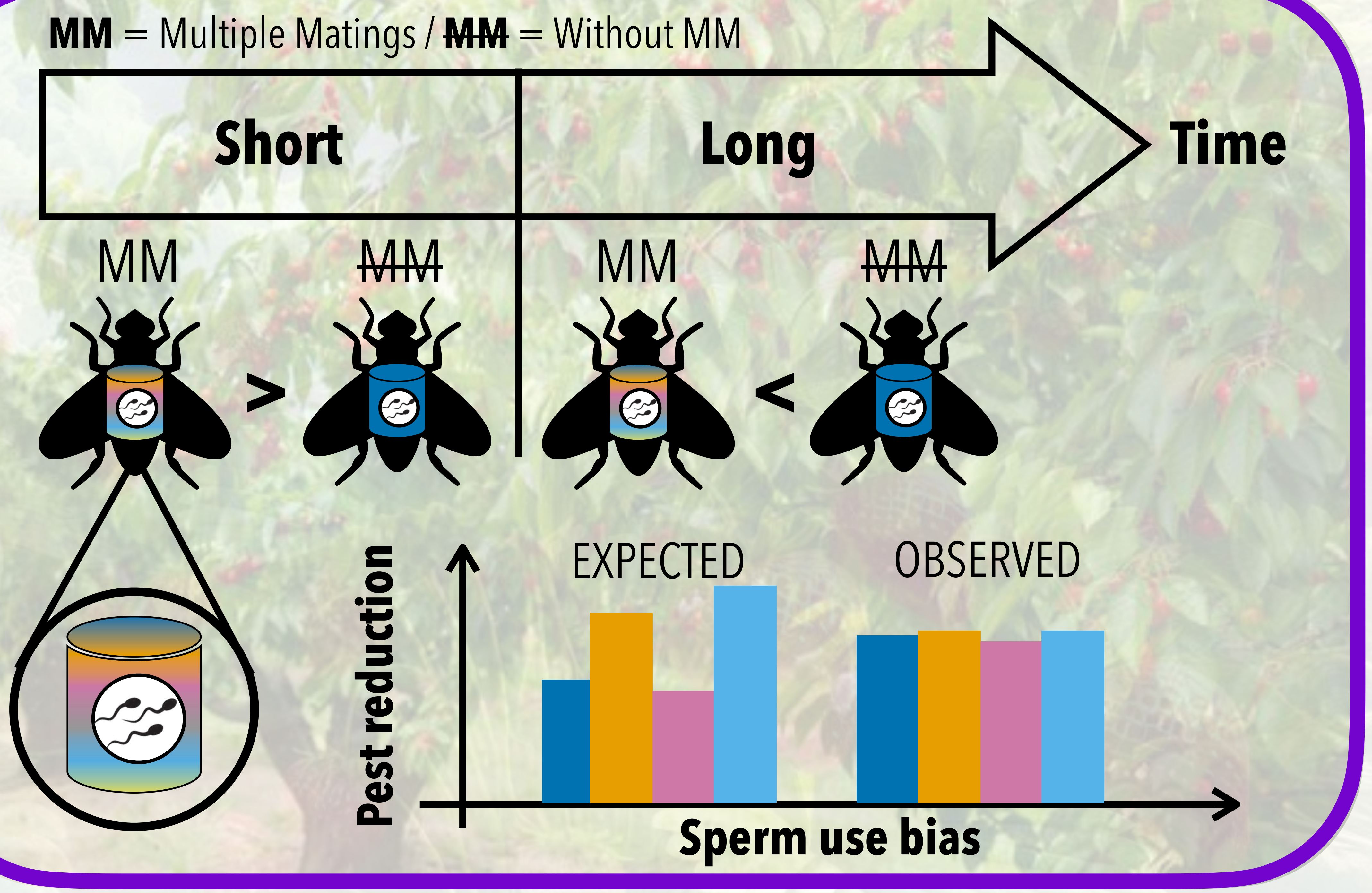
STERILIZATION



Exposure to ionizing radiation

MASS RELEASES

DILUTION OF WILD POPULATIONS



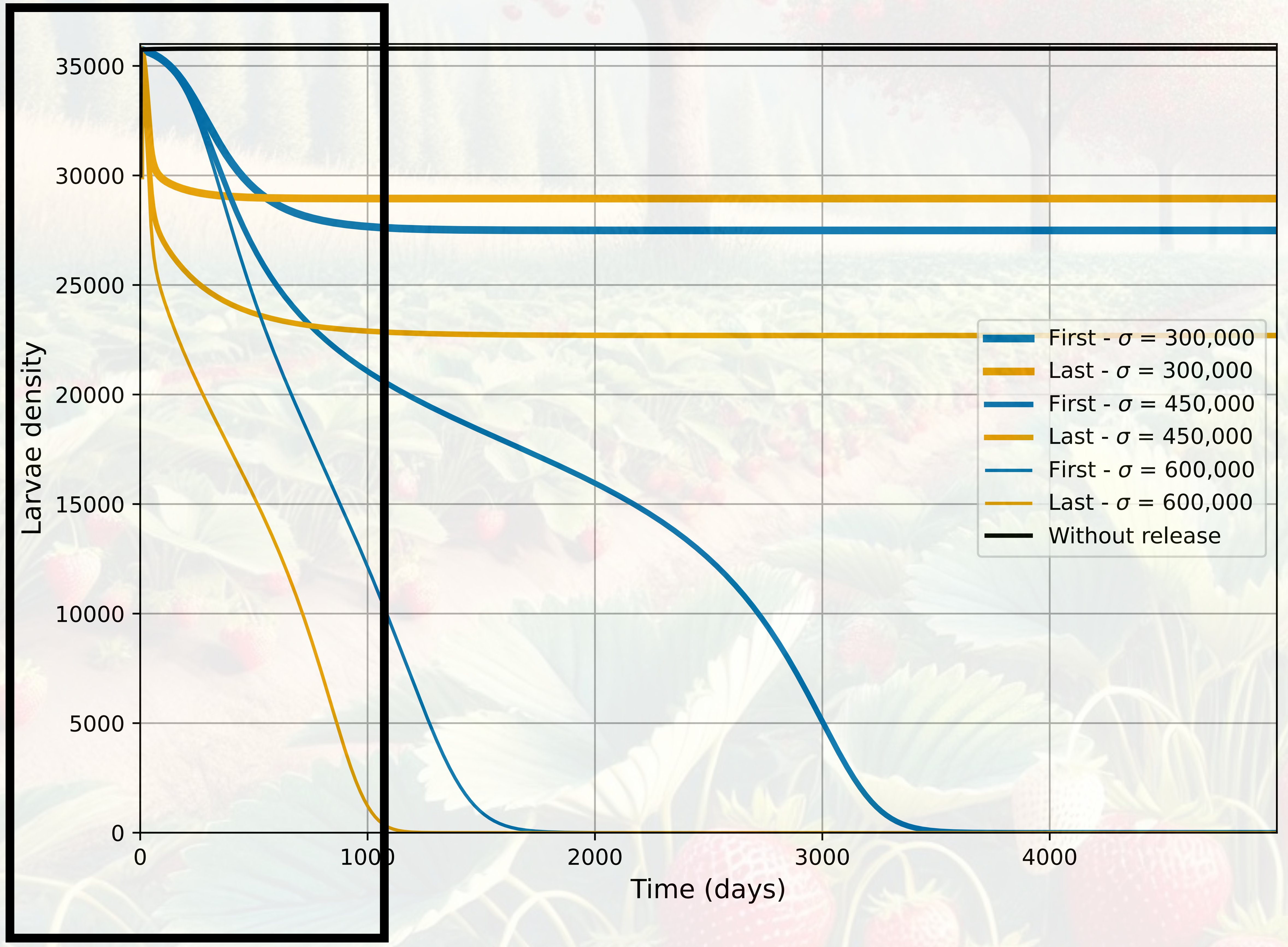
Institut Sophia Agrobiotech
SANTE DES PLANTES - ENVIRONNEMENT
INRAE
Inria
UNIVERSITÉ CÔTE D'AZUR
cnrs
SMAI
société de mathématiques appliquées et industrielles

THANK YOU!

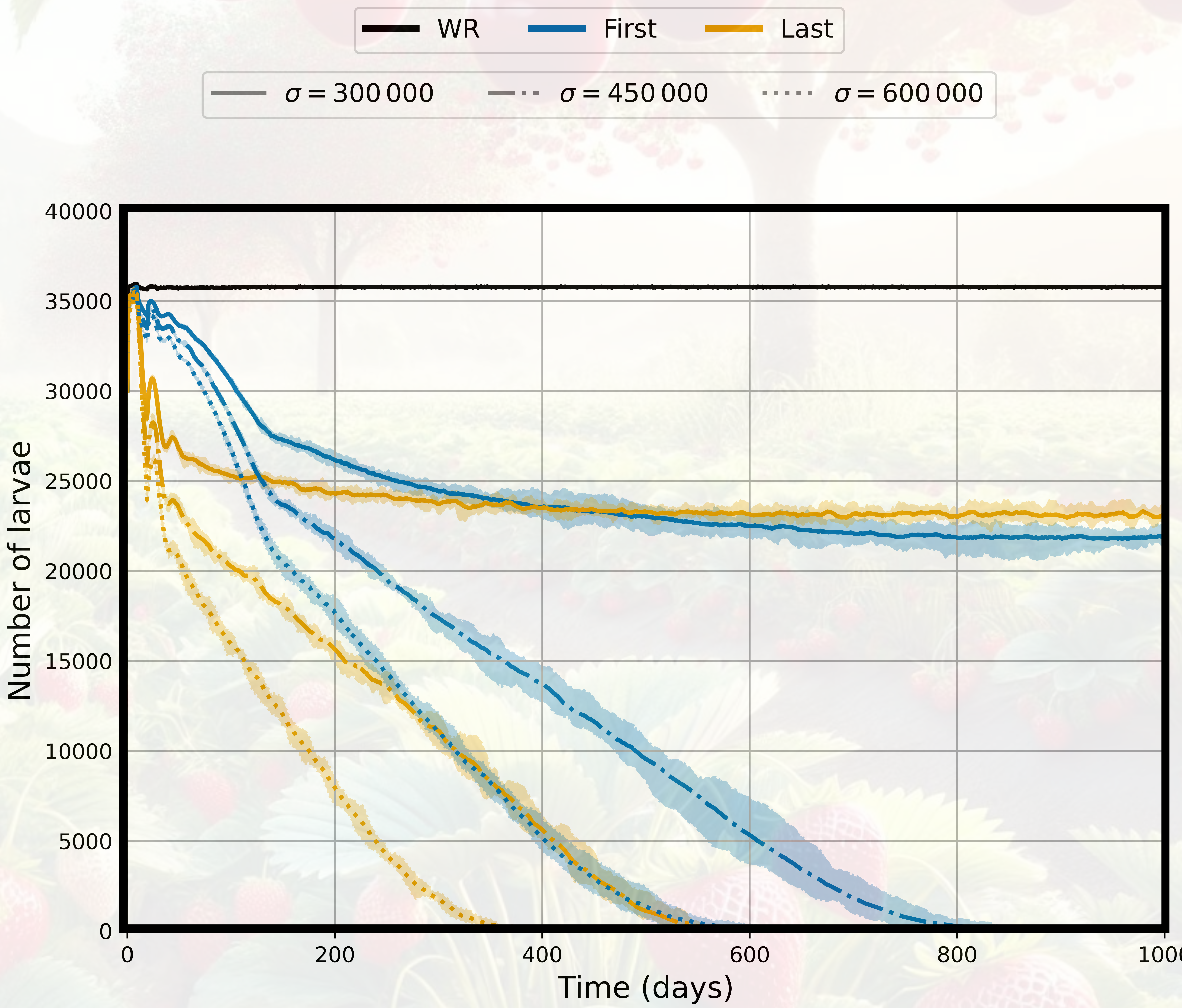
Marine Courtois (INRAE Sophia Antipolis, France)


Automne - Hiver
Printemps - Eté
Sans traitement
Temps
Traitement phytosanitaire (Phyto)*
Temps
Filets
Temps
Technique de l'Insecte Stérile (TIS)
Temps
Parasitoïdes
Acclimatation
Augmentorium
Temps
Prophylaxie, Piégeage
Temps
Les barres indiquent les périodes de travail, leur épaisseur reflète la quantité réalisée.
LEVIER SIMPLE
% de dégâts
Temps
APPROCHES MULTI-LEVIERS
Synergies potentielles - Combinaisons hypothétiques
Filets + Phyto
Parasitoïdes +TIS
Parasitoïdes + Filets + Prophylaxie + TIS
Combinaisons qui pourraient s'avérer inefficaces
Phyto + TIS
Phyto + Parasitoïdes
● Les courbes présentées sont hypothétiques et schématiques, établies à partir des données issues de la littérature.
● Les leviers d'action illustrés sont également simplifiés et ne reflètent pas pleinement la complexité de leur mise en œuvre réelle.
* Les produits phytosanitaires induisent un risque de résistance.

Compartmental model



Agent-based model



APPENDIX

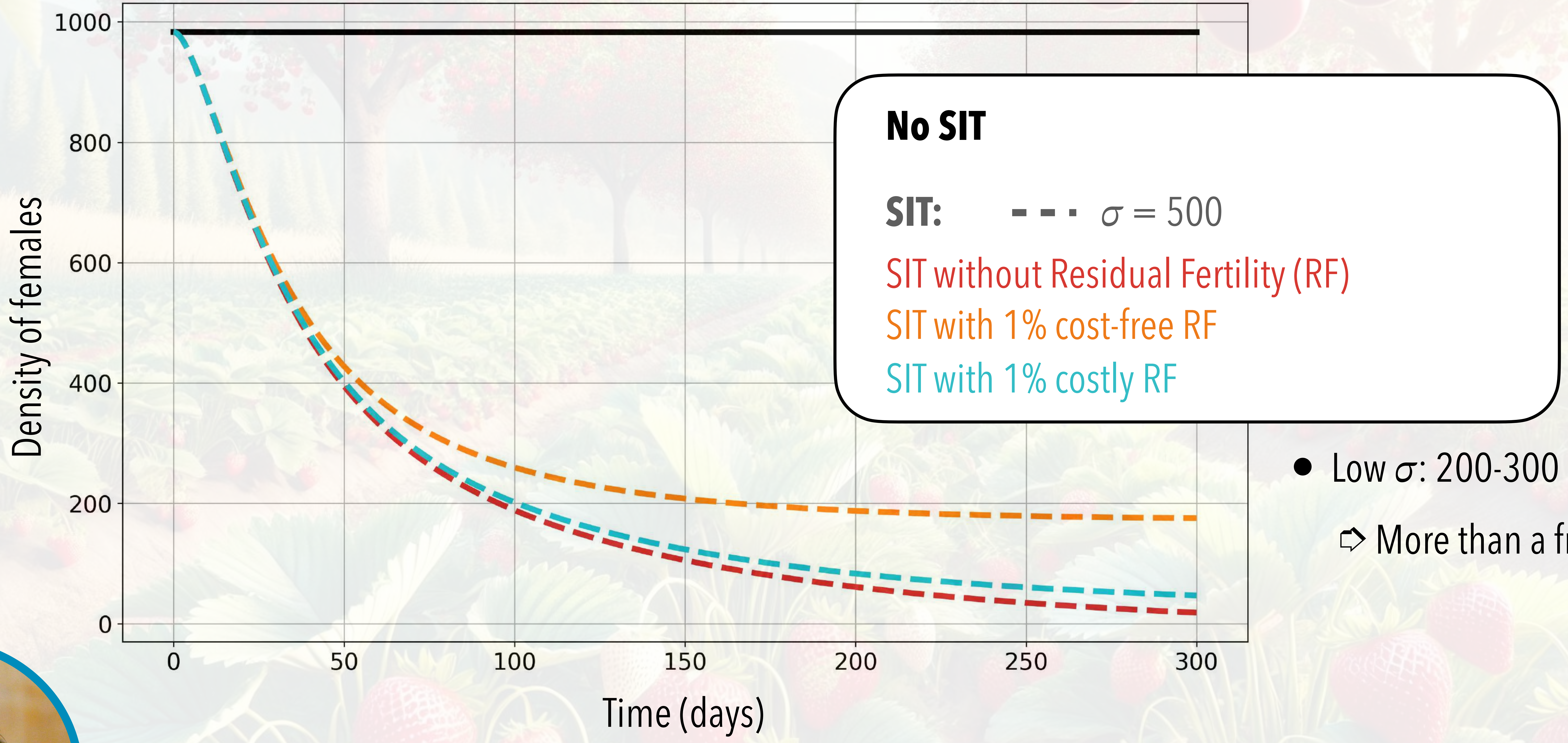
Biological parameters - *Ceratitis capitata*

Parameters	Descriptions	Values & [Range]	Units
μ_F	Female mortality rate[1,6]	0.050 [0.018 - 0.083]	day^{-1}
μ_M	Male mortality rate[1,6]	0.036 [0.014 - 0.057]	day^{-1}
μ_S	Sterilized male mortality rate[2,6]	0.057 [0.037 - 0.077]	day^{-1}
p	Sex ratio[3]	0.500 [0.450 - 0.550]	-
r	Emergence rate[4,6]	23.7 [19.2 - 28.5]	day^{-1}
k	Mating half-saturation constant[5]	1 [0.01 - 100]	ind.ha^{-1}
$1-\eta$	Sterilization cost[5]	0.8 [0 - 1]	-
β	Oviposition competition between females[6]	0.24 [0.18 - 0.30]	(ind.ha^{-1})$^{-1}$
σ	Sterilized male release rate[7]	250 [0.01 - 500]	ind.ha^{-1}.day^{-1}
δ	Proportion of non-sterile males among the releases[7] (cost-free fertility)	0.5 [0.01 - 1]	-
ϵ	Proportion of non-sterile males among the releases[7] (costly fertility)	0.5 [0.01 - 1]	-

Ceratitis capitata

(1) **Residual fertility**: imperfect sterilization

- **Convergence time**



- Low σ: 200-300 days
  - ➪ More than a fruit season

Ceratitis capitata

(1) **Residual fertility**: imperfect sterilization

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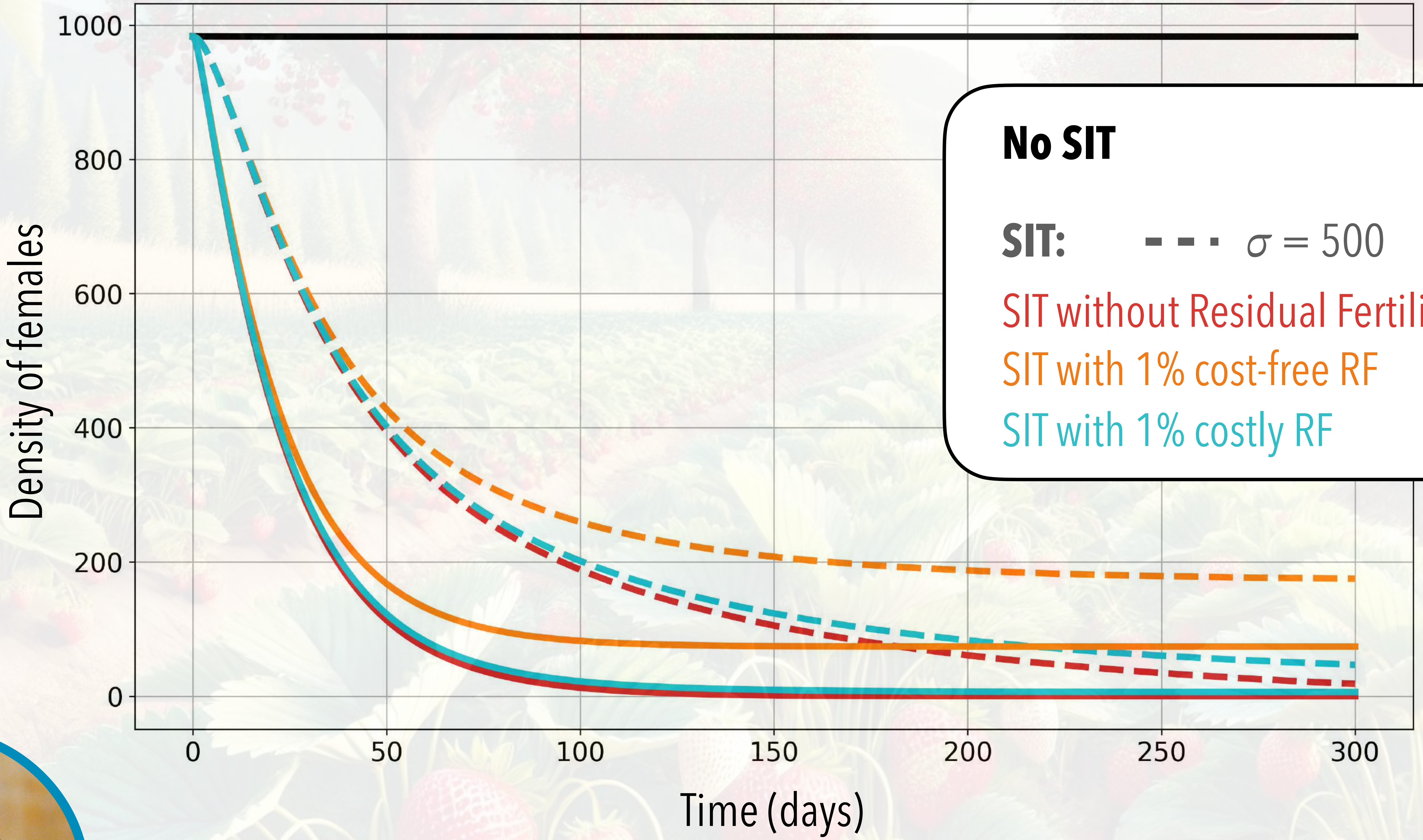


- Low σ: 200-300 days
  - ➪ More than a fruit season
- High σ: 75 days

Ceratitis capitata

(2) **Multiple matings**: ability for females to mate and re-mate

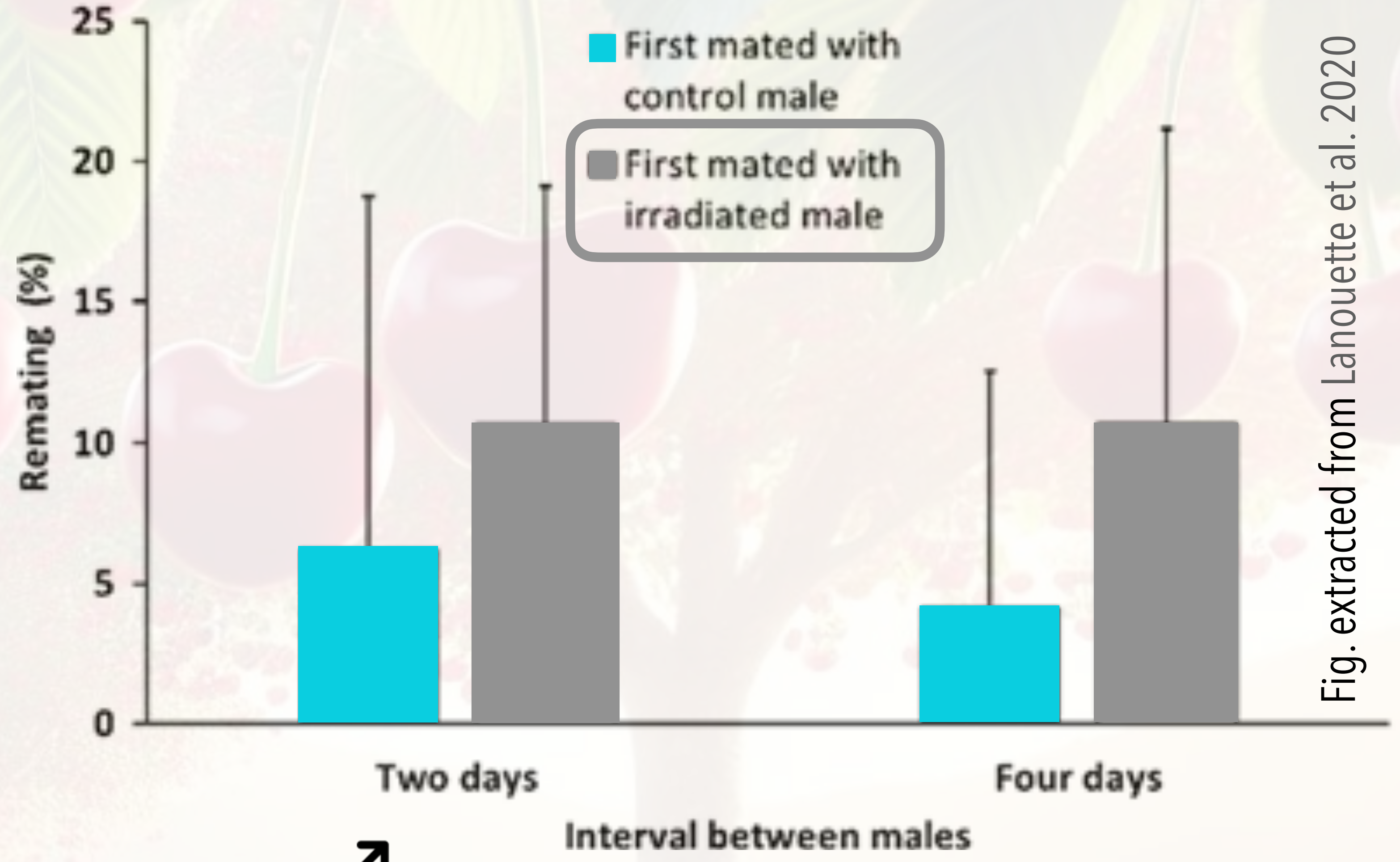
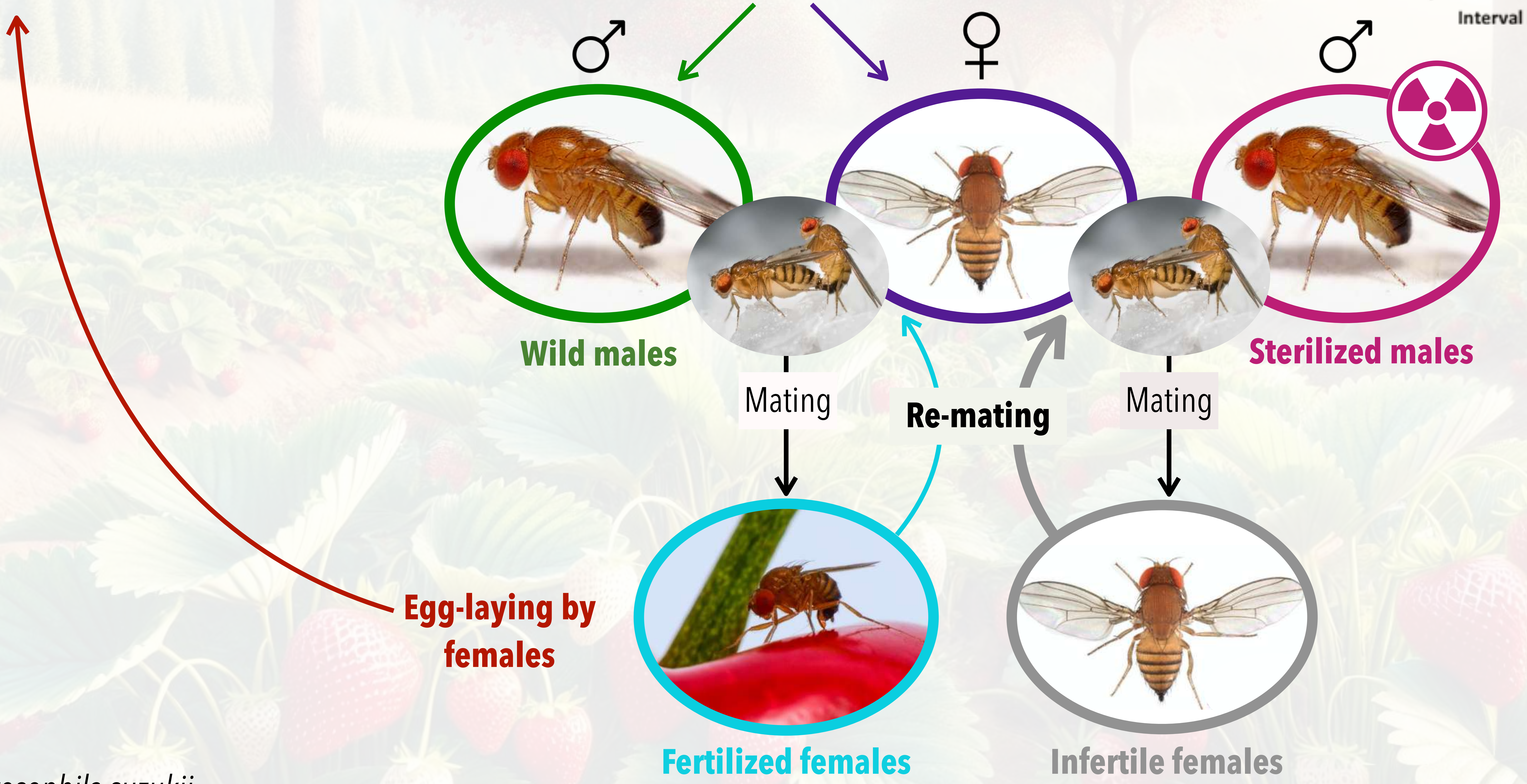


Fig. extracted from Lanouette et al. 2020



Drosophila suzukii

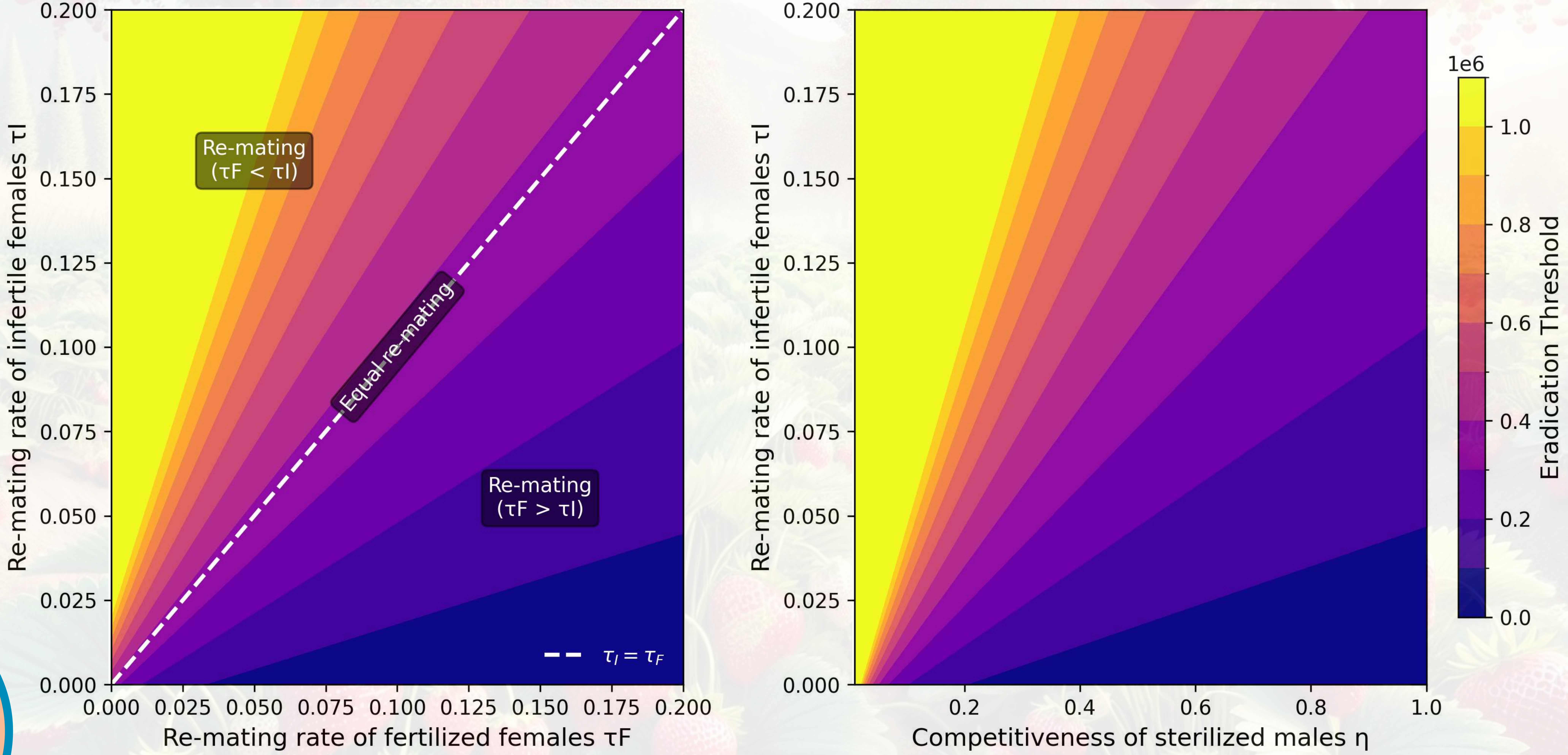
Biological parameters - *Drosophila suzukii*

Parameter/Description	Value and [Range]	Unit	Reference
μ_L (Larvae mortality rate)	0.362 [0.353 - 0.372]	day^{-1}	(Emiljanowicz *et al.*, 2014)
μ_F (Female mortality rate)	0.012 [0.006 - 0.053]	day^{-1}	(Papanastasiou *et al.*, 2021)
μ_M (Male mortality rate)	0.013 [0.007 - 0.042]	day^{-1}	(Papanastasiou *et al.*, 2021)
μ_S (Sterilized male mortality rate)	0.054 [0.028 - 1]	day^{-1}	(Lanouette *et al.*, 2017)
ω (Egg-laying rate)	5.70 [5.46 - 5.94]	eggs per female per day	(Emiljanowicz *et al.*, 2014)
ν (Larvae hatching rate)	0.166 [0.163 - 0.168]	day^{-1}	(Emiljanowicz *et al.*, 2014)
p (Sex ratio)	0.50 [0.45 - 0.55]	-	(Emiljanowicz *et al.*, 2014)
χ (Mating rate)	-	day^{-1}	Assumed high[1]
$1-\eta$ (Sterilization cost)	0.40 [0.37 - 0.62]	-	(Lanouette *et al.*, 2020)
K (Carrying capacity)	36,000	larvae per hectare	Calculated[2]
σ (Sterilized male release rate)	1,000 [200 - 1,200]	$ind.day^{-1}.ha^{-1}$	(Homem *et al.*, 2022)
τ_F (Re-mating rate of fertilized females)	0.12 [0.08 - 0.33]	day^{-1}	(Krüger *et al.*, 2019)
τ_I (Re-mating rate of sterilized females)	0.13 [0.09 - 0.25]	day^{-1}	(Krüger *et al.*, 2019)

Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Remating ($\tau_I < \tau_F$) > Without remating = Equal remating > Remating ($\tau_I > \tau_F$) > Remating of infertile females only ($\tau_I > \tau_F = 0$)



Drosophila suzukii

(2) **Multiple matings**: ability for females to mate and re-mate

Are multiple matings incompatible with SIT?

- Development of an **agent-based model** to explore how potential **sperm use biases** impact pest control with SIT

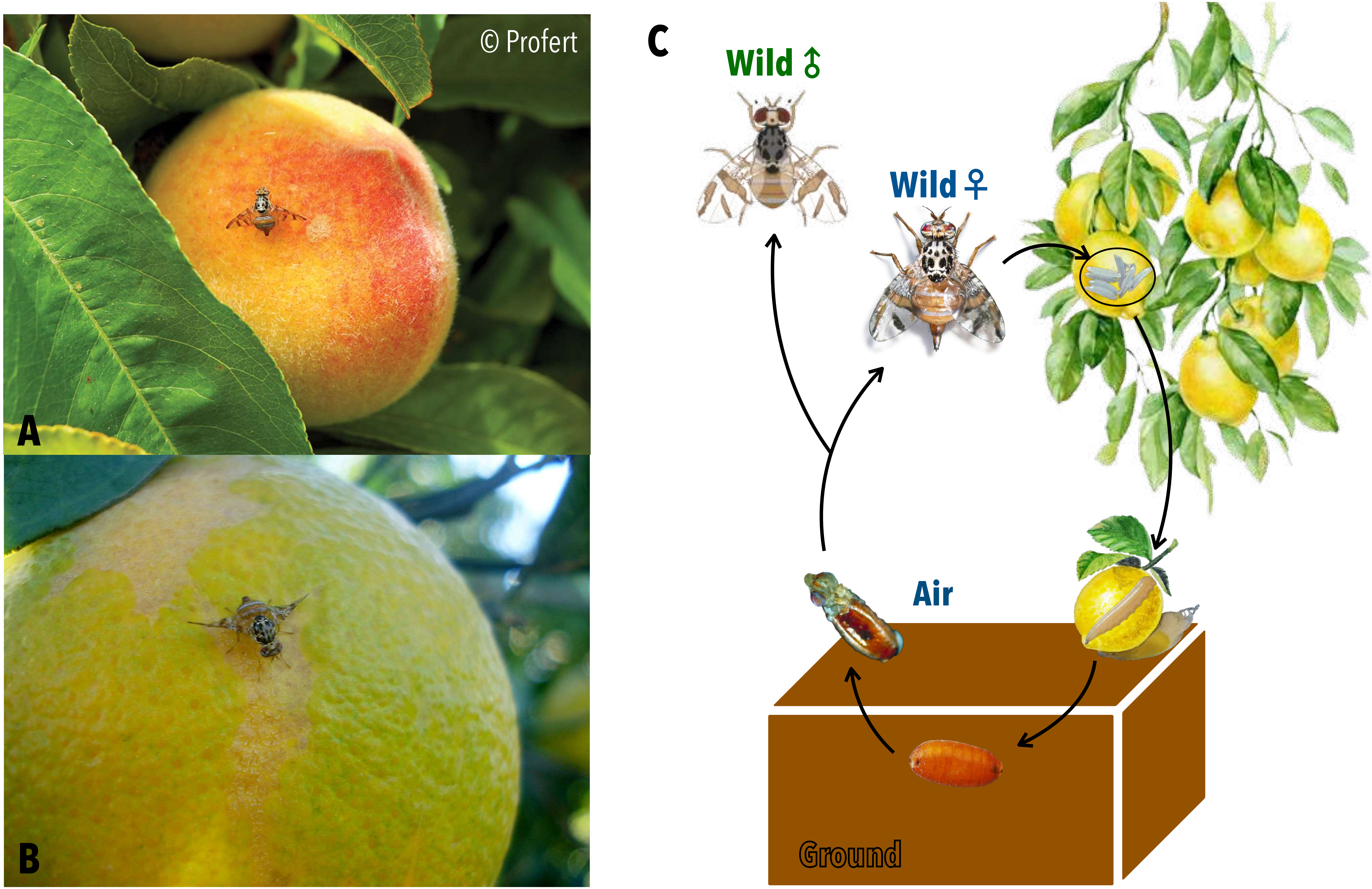
STERILE MALES (S)
unique_id (real integer)
creation_date (real integer)
death_date (real integer)

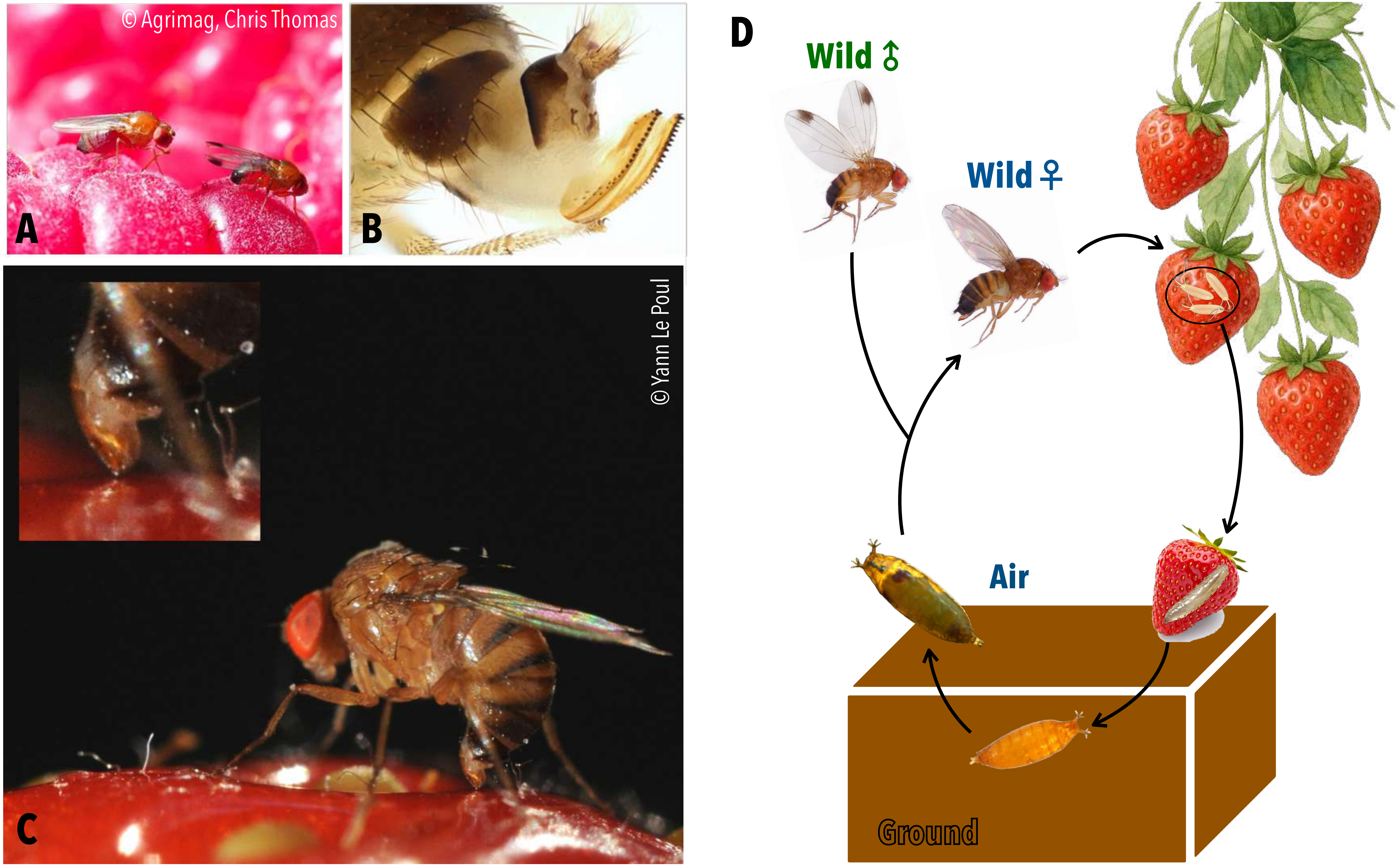
WILD MALES (W)
unique_id (real integer)
creation_date (real integer)
death_date (real integer)

LARVAE (L)
unique_id (real integer)
creation_date (real integer)
emergence_date (real integer)

FEMALES (F)
unique_id (real integer)
creation_date (real integer)
death_date (real integer)
time_until_next_mating (real integer)
spermatheca (list of -1 initially)
eggs_laid (real integer)

Drosophila suzukii


© Profert
A
B
C
Wild ♂
Wild ♀
Air
Ground



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