Supporting Information

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SI Text

Nondimensionalization. The differential equation system of the model for development of huanglongbing in a citrus tree is given by (see Fig. 1 for the meaning of the symbols)

$$\left.\begin{aligned}
\frac{dE}{dt} &= \alpha\left(A^{\mathrm{u}} + A_1^{\mathrm{i}} + A_2^{\mathrm{i}}\right)\frac{H}{P} - (\delta_{\mathrm{e}} + \sigma)E\\
\frac{dN^{\mathrm{u}}}{dt} &= \sigma E - \beta_{\mathrm{n}} N^{\mathrm{u}}\frac{X + \theta_2 Y}{P} - (\delta_{\mathrm{n}} + \gamma)N^{\mathrm{u}}\\
\frac{dN^{\mathrm{i}}}{dt} &= \beta_{\mathrm{n}} N^{\mathrm{u}}\frac{X + \theta_2 Y}{P} - (\delta_{\mathrm{n}} + \gamma)N^{\mathrm{i}}\\
\frac{dA^{\mathrm{u}}}{dt} &= \gamma N^{\mathrm{u}} - \beta_{\mathrm{a}} A^{\mathrm{u}}\frac{X + \theta_2 Y}{P} - (\delta_{\mathrm{a}} + \kappa)A^{\mathrm{u}}\\
\frac{dA_1^{\mathrm{i}}}{dt} &= \beta_{\mathrm{a}} A^{\mathrm{u}}\frac{X + \theta_2 Y}{P} - (\delta_{\mathrm{a}} + \kappa)A_1^{\mathrm{i}}\\
\frac{dA_2^{\mathrm{i}}}{dt} &= \gamma N^{\mathrm{i}} - (\delta_{\mathrm{a}} + \kappa)A_2^{\mathrm{i}}\\
\frac{dH}{dt} &= \xi(t)H - \beta_{\mathrm{p}} H\frac{\left(A_1^{\mathrm{i}} + \theta_1 A_2^{\mathrm{i}}\right)}{P} - \lambda H\frac{(X + \theta_2 Y)}{P} - \delta_{\mathrm{p}} H\\
\frac{dW}{dt} &= \beta_{\mathrm{p}} H\frac{\left(A_1^{\mathrm{i}} + \theta_1 A_2^{\mathrm{i}}\right)}{P} + \lambda H\frac{(X + \theta_2 Y)}{P} - (\eta_1 + \delta_{\mathrm{p}})W\\
\frac{dX}{dt} &= \eta_1 W - (\eta_2 + \delta_{\mathrm{p}})X\\
\frac{dY}{dt} &= \eta_2 X - \delta_{\mathrm{p}} Y.
\end{aligned}\right\} \quad [S1]$$

We note that $P = H + W + X + Y$. Let

$$\tilde{H} = \frac{H}{P}, \tilde{W} = \frac{W}{P}, \tilde{X} = \frac{X}{P}, \tilde{Y} = \frac{Y}{P},$$

and

$$\tilde{E} = \frac{E}{P}, \tilde{N}^{\mathrm{u}} = \frac{N^{\mathrm{u}}}{P}, \tilde{N}^{\mathrm{i}} = \frac{N^{\mathrm{i}}}{P}, \tilde{A}^{\mathrm{u}} = \frac{A^{\mathrm{u}}}{P}, \tilde{A}_1^{\mathrm{i}} = \frac{A_1^{\mathrm{i}}}{P}, \tilde{A}_2^{\mathrm{i}} = \frac{A_2^{\mathrm{i}}}{P}. \quad [S2]$$

The variables $\tilde{H}$, $\tilde{W}$, $\tilde{X}$, and $\tilde{Y}$ are fractions of the total flush population such that $\tilde{H} + \tilde{W} + \tilde{X} + \tilde{Y} = 1$ + and $\tilde{E}$, $\tilde{N}^{\mathrm{u}}$, $\tilde{N}^{\mathrm{i}}$, $\tilde{A}^{\mathrm{u}}$, $\tilde{A}_1^{\mathrm{i}}$, $\tilde{A}_2^{\mathrm{i}}$ are the densities of the vectors in the respective classes per flush. We note that the rate of change of the total flush population $dP/dt \neq 0$ but $dP/dt = \xi(t)H - \delta_{\mathrm{p}}P$. Substituting the new variables into model system (Eq. **S1**) and dropping the tildes (~), the equations for the proportion of flushes and vector populations per flush become

$$\left.\begin{aligned}
\frac{dE}{dt} &= \alpha\left(A^{\mathrm{u}} + A_1^{\mathrm{i}} + A_2^{\mathrm{i}}\right)H - (\delta_{\mathrm{e}} + \sigma)E + \left(\delta_{\mathrm{p}} - \xi(t)H\right)E\\
\frac{dN^{\mathrm{u}}}{dt} &= \sigma E - \beta_{\mathrm{n}} N^{\mathrm{u}}(X + \theta_2 Y) - (\delta_{\mathrm{n}} + \gamma)N^{\mathrm{u}} + \left(\delta_{\mathrm{p}} - \xi(t)H\right)N^{\mathrm{u}}\\
\frac{dN^{\mathrm{i}}}{dt} &= \beta_{\mathrm{n}} N^{\mathrm{u}}(X + \theta_2 Y) - (\delta_{\mathrm{n}} + \gamma)N^{\mathrm{i}} + \left(\delta_{\mathrm{p}} - \xi(t)H\right)N^{\mathrm{i}}\\
\frac{dA^{\mathrm{u}}}{dt} &= \gamma N^{\mathrm{u}} - \beta_{\mathrm{a}} A^{\mathrm{u}}(X + \theta_2 Y) - (\delta_{\mathrm{a}} + \kappa)A^{\mathrm{u}} + \left(\delta_{\mathrm{p}} - \xi(t)H\right)A^{\mathrm{u}}\\
\frac{dA_1^{\mathrm{i}}}{dt} &= \beta_{\mathrm{a}} A^{\mathrm{u}}(X + \theta_2 Y) - (\delta_{\mathrm{a}} + \kappa)A_1^{\mathrm{i}} + \left(\delta_{\mathrm{p}} - \xi(t)H\right)A_1^{\mathrm{i}}\\
\frac{dA_2^{\mathrm{i}}}{dt} &= \gamma N^{\mathrm{i}} - (\delta_{\mathrm{a}} + \kappa)A_2^{\mathrm{i}} + \left(\delta_{\mathrm{p}} - \xi(t)H\right)A_2^{\mathrm{i}}\\
\frac{dH}{dt} &= \xi(t)H(1 - H) - \beta_{\mathrm{p}} H\left(A_1^{\mathrm{i}} + \theta_1 A_2^{\mathrm{i}}\right) - \lambda H(X + \theta_2 Y)\\
\frac{dW}{dt} &= \beta_{\mathrm{p}} H\left(A_1^{\mathrm{i}} + \theta_1 A_2^{\mathrm{i}}\right) + \lambda H(X + \theta_2 Y) - (\eta_1 + \xi(t)H)W\\
\frac{dX}{dt} &= \eta_1 W - (\eta_2 + \xi(t)H)X\\
\frac{dY}{dt} &= \eta_2 X - \xi(t)HY.
\end{aligned}\right\} \quad [S3]$$

The disease-free equilibrium of the model system (Eq. **S3**) is

$$\begin{aligned}
\varepsilon_0 &= \left(\hat{E}, \hat{N}^{\mathrm{u}}, \hat{N}^{\mathrm{i}}, \hat{A}^{\mathrm{u}}, \hat{A}_1^{\mathrm{i}}, \hat{A}_2^{\mathrm{i}}, \hat{H}, \hat{W}, \hat{X}, \hat{Y}\right)\\
&= \left(\hat{E}, \frac{\sigma\hat{E}}{\delta_{\mathrm{n}} + \gamma + \bar{\xi} - \delta_{\mathrm{p}}}, 0, \frac{\gamma\hat{N}^{\mathrm{u}}}{\delta_{\mathrm{a}} + \kappa + \bar{\xi} - \delta_{\mathrm{p}}}, 0, 0, 1, 0, 0, 0\right), \quad [S4]
\end{aligned}$$

where $\hat{E}$ is the egg population at the disease-free equilibrium, and $(\delta_{\mathrm{n}} + \gamma) + \bar{\xi} - \delta_{\mathrm{p}} > 0$, $(\delta_{\mathrm{a}} + \kappa) + \bar{\xi} - \delta_{\mathrm{p}} > 0$, and $\delta_{\mathrm{e}} + \sigma + \bar{\xi} - \delta_{\mathrm{p}} > 0$.

The expression $(\xi - \delta_{\mathrm{p}})$ gives the net growth rate constant of the flush population in a disease-free population. In the absence of HLB infection, the population size $P(t)$ declines exponentially to 0 if $(\xi - \delta_{\mathrm{p}}) < 0$, remains constant if $(\xi - \delta_{\mathrm{p}}) = 0$, and grows exponentially if $(\xi - \delta_{\mathrm{p}}) > 0$.

Reproductive Number. The expression for the reproductive number $\mathcal{R}_0$ of the plant-vector model (Eq. **S3**) is given by

$$\mathcal{R}_0 = Q_1 + \sqrt{Q_2 + Q_1^2}, \quad [S5]$$

where

$$\begin{aligned}
Q_1 &= \frac{\eta_1\lambda(\bar{\xi} + \eta_2\theta_2)}{2\bar{\xi}(\eta_1 + \bar{\xi})(\eta_2 + \bar{\xi})} \text{ and}\\
Q_2 &= \frac{\beta_{\mathrm{p}}\eta_1(\eta_2\theta_2 + \bar{\xi})\left(\beta_{\mathrm{n}}\gamma\theta_1\hat{N}^{u} + \beta_{\mathrm{a}}\left(\gamma + \delta_{\mathrm{n}} + \bar{\xi} - \delta_{\mathrm{p}}\right)\hat{A}^{u}\right)}{\bar{\xi}\left(\gamma + \delta_{\mathrm{n}} + \bar{\xi} - \delta_{\mathrm{p}}\right)(\eta_1 + \bar{\xi})(\eta_2 + \bar{\xi})\left(\kappa + \delta_{\mathrm{a}} + \bar{\xi} - \delta_{\mathrm{p}}\right)}.
\end{aligned}$$

The parameter $\bar{\xi} = 1/T\int_0^T \xi(v)dv$ is the average value of the maturation rate of the flush population taken over a cycle of period T. It has been shown in several studies that in some nonautonomous epidemic models, expressed in terms of differential equations the basic reproductive number can be obtained from the corresponding autonomous model by using time averages of the coefficients (1–4).

The reproductive number $\mathcal{R}_0$ can also be derived using heuristic arguments as follows. If an infected adult vector (in the A_1^{i} state) is introduced into a population of susceptible flush, it infects the flush at a rate β_{p} over its infectious period $1/(\kappa + \delta_{\mathrm{a}} + \bar{\xi} - \delta_{\mathrm{p}})$. The probability that the infected flush becomes infectious is $\eta_1/(\eta_1 + \bar{\xi})$. The average number of flush that become infectious is

$$\mathcal{R}_P^{A_1} = \beta_{\mathrm{p}}\frac{1}{\left(\kappa + \delta_{\mathrm{a}} + \bar{\xi} - \delta_{\mathrm{p}}\right)}\frac{\eta_1}{(\eta_1 + \bar{\xi})}. \quad [S6]$$

If, on the other hand, there is an infectious asymptomatic flush and a population of adult vectors, the vectors become infected at a rate $\beta_{\mathrm{a}}\hat{A}^{\mathrm{u}}$ over the infectious period of the flush $1/(\eta_2 + \bar{\xi})$. The asymptomatic infectious flush becomes symptomatic at a rate η_2. In the symptomatic state the flush infects vectors at a rate $\beta_{\mathrm{a}}\theta_2\hat{A}^{\mathrm{u}}$ over the infectious period $1/\bar{\xi}$. Therefore, the number of adult vectors that become infectious is

$$\mathcal{R}_{A_1}^P = \beta_{\mathrm{a}}\hat{A}^{\mathrm{u}}\frac{1}{\eta_2 + \bar{\xi}} + \beta_{\mathrm{a}}\theta_2\hat{A}^{\mathrm{u}}\frac{\eta_2}{\eta_2 + \bar{\xi}}\frac{1}{\bar{\xi}}. \quad [S7]$$

Following similar arguments, the number of infected adults that were infected in the nymph stages is

$$\mathcal{R}_{A_2}^{P} = \beta_{\mathrm{n}}\hat{N}^{\mathrm{u}}\frac{\gamma}{(\gamma+\delta_{\mathrm{n}}+\bar{\xi}-\delta_{\mathrm{p}})}\frac{1}{(\eta_2+\bar{\xi})}\left(1+\frac{\eta_2\theta_2}{\bar{\xi}}\right), \qquad \textbf{[S8]}$$

and the number of flush infected by the adults in the A_2^{i} class is

$$\mathcal{R}_{P}^{A_2} = \beta_{\mathrm{p}}\theta_1\frac{1}{(\kappa+\delta_{\mathrm{a}}+\bar{\xi}-\delta_{\mathrm{p}})}\frac{\eta_1}{(\eta_1+\bar{\xi})}. \qquad \textbf{[S9]}$$

Therefore, the average number of infected vectors that arise from a single infected vector without the infection from flush to flush is $Q_2 = \mathcal{R}_P^{A_1}\mathcal{R}_{A_1}^{P} + \mathcal{R}_P^{A_2}\mathcal{R}_{A_2}^{P}$. Following the above arguments, it is clear that the average number of infected flush from a single infected flush is $2Q_1$ in the absence of the vector population. A similar approach of finding the reproductive number for a vector-transmitted disease was considered elsewhere (5).

Parameter Values. To obtain some of the parameter values, we used information for mean developmental periods and survivorship of immature stages of *D. citri* from Table S1, part of which was extracted from Liu and Tsai (6). To estimate the rate of mortality of nymphs, the sum of the survivorship proportion of each of the five nymphal stages was divided by five to obtain the average survivorship for the nymphs. The result was subtracted from 1 to get the probability of death and divided by the number of days taken by the nymphs to become adults. The value obtained gives the mortality rate of nymphs per day, δ_{n}. The same approach was used to obtain the parameter for the rate at which eggs become nonviable, δ_{e}. Several studies have shown that it might take 15–30 min for adults to acquire the bacteria (7, 8) but reports on acquisition vary widely. We assume that nymphs would take much longer to acquire the bacteria than the adults because of the shorter piercing mouths of young nymphs. Therefore, the acquisition time for nymphs, π_{n}, is assumed to be 2 h.

Sensitivity Analysis. Relative importance of model parameters to disease transmission and prevalence is determined through sensitivity analysis. Sensitivity analysis of parameters is commonly carried out to determine robustness of model predictions to variation in parameter values. The parameters that are crucial in the model are those that appear in the reproductive number $\mathcal{R}_0$ because these parameters influence the number of secondary infections either positively or otherwise. They should be considered whenever intervention strategies are to be implemented. The ratio of the relative change in a variable to the relative change in a parameter is the normalized forward sensitivity index of the variable to that parameter. The variable in this case is the reproductive number, which is a differentiable function of the parameters. Therefore, sensitivity indexes may alternatively be defined using partial derivatives (9). For example, the computation of the sensitivity index of $\mathcal{R}_0$ with respect to the within-tree transmission rate λ using parameter values in Table 1 is given by

$$\Upsilon_{\lambda}^{\mathcal{R}_0} = \left(\frac{\partial\mathcal{R}_0}{\partial\lambda}\right)\left(\frac{\lambda}{\mathcal{R}_0}\right) = 0.9373 > 0. \qquad \textbf{[S10]}$$

The value 0.9373 shows that $\mathcal{R}_0$ is an increasing function of λ. The sensitivity indexes of the remaining parameters are shown in Table 2.

Three parameters associated with tree characteristics, namely maturation rate of flush ($\bar{\xi}$), internal movement of the pathogen within the tree λ, and latent period $1/\eta_1$, are all very influential on the value of $\mathcal{R}_0$ (Table 2). When λ is reduced, the dynamics of HLB development change drastically from continued expansion of HLB symptoms to a dynamic equilibrium between healthy, asymptomatic, and symptomatic flush (Fig. 3). When the latent period is varied between 30 and 180 d, there are large differences in the maximal proportions of asymptomatic flush attained (35–60%) (Fig. S1*A*), but there are only slight differences in the time needed to reach 100% symptomatic flush (Fig. S1*B*).

Scenario Analysis. If an insecticide is applied starting from 360 d or 450 d after initial infection, increases in the proportion of healthy flush and decreases in the proportion of asymptomatic infected flush ensue (Fig. 4 *A* and *B*). Although early spraying reduces the temporal increase in infected flush, it does not eliminate the pathogen from a tree (Fig. 4*B*). As expected, spraying the vectors reduces the psyllid populations in all categories, but they continue to oscillate (Fig. S2).

If insecticides are applied when $\lambda = 0.25$, all flush and vector categories continue to oscillate similar to the nonsprayed scenario (Fig. S3). However, the populations of adult psyllids are reduced from a maximum of 4.5 to 4.3 individuals per flush (Fig. S3*A*) and the maximum proportion of symptomatic flush is reduced from 0.35 to 0.29 (Fig. S3*B*). Thus, if internal resistance to infection is high, spraying the psyllids will not have a great impact on the dynamics of the populations.

The effects of varying internal movement of the bacteria λ, on both healthy and symptomatic flush are shown in Fig. S4. The great variability in the flush population caused by small changes in λ shows how sensitive the model is to that parameter. The results shown in Fig. S4 confirm the analysis obtained from sensitivity analysis on sensitivity of $\mathcal{R}_0$ to λ.

When initial conditions of flush populations are varied with and without periodic forcing, different end points are obtained. Fig. S5 shows how changing the initial conditions of the healthy and latent flush affect the end point of the dynamics of the model without and with periodic forcing. In the absence of periodic forcing, that is, when strength of seasonality $\upsilon = 0$, varying initial conditions always results in the 100% symptomatic state. However, when periodic forcing is present, changing the initial conditions results in either an oscillatory state (all populations present and oscillating) or a 100% symptomatic state. Thus, periodic forcing affects the dynamics of the model. However, periodic forcing for growth of flush was included, because it is observed in the field that flush appearance and growth are seasonal (10).

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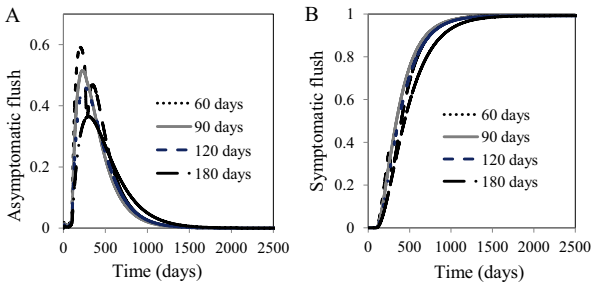

Fig. S1. (*A* and *B*) Proportion of asymptomatic flush (*A*) and symptomatic flush (*B*) when latent period is varied from 60 d to 180 d. The parameter for internal movement of the pathogen in the tree is $\lambda = 0.33$.

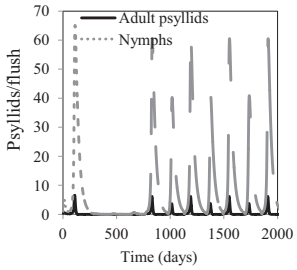

Fig. S2. Populations of total adult psyllids and nymphs per flush when psyllids are sprayed twice a year with an insecticide that is 0.75 effective, at 360 d after initial infection. The input rate of healthy flush follows a periodic function with two peaks in 1 y. The parameter for internal movement of the pathogen in the tree is $\lambda = 0.33$.

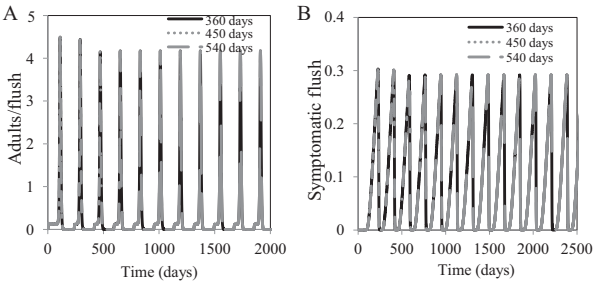

Fig. S3. (*A* and *B*) Proportion of symptomatic flush (*A*) and adult psyllids (*B*) when psyllids are sprayed twice a year with an insecticide that is 0.75 effective, 360 d, 450 d, and 540 d after initial infection. The parameter for internal movement of the pathogen in the tree is $\lambda = 0.25$.

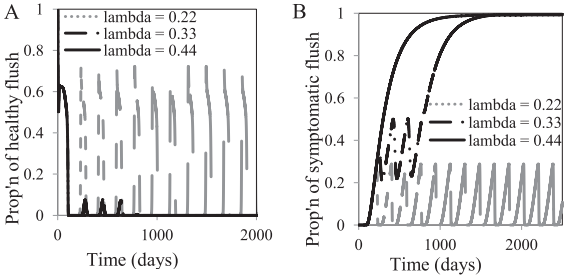

Fig. S4. (*A* and *B*) Proportion of healthy flush (*A*) and symptomatic flush (*B*) when λ has values of 0.22, 0.33, and 0.44. All of the other parameters are as shown in Table 1.

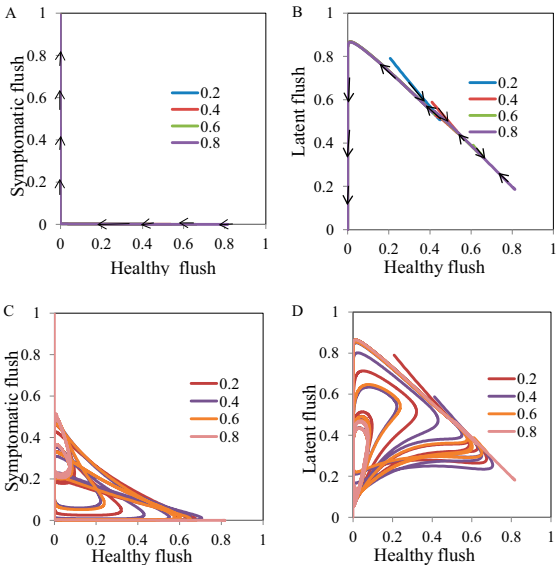

Fig. S5. (*A*–*D*) Phase plane portraits of healthy (*H*) and symptomatic (*Y*) flush (*A* and *C*) and of healthy (*H*) and latent (*W*) flush (*B* and *D*). *A* and *B* are obtained when periodic forcing is zero and *C* and *D* are obtained when periodic forcing is present. Initial conditions of the healthy and latent flush were varied. The values show the different initial conditions of healthy flush and those of latent flush are known by subtracting these values from one. All of the other parameters are as shown in Table 1.

Table S1. Survivorship and developmental stages of immature stages of *D. citri* at 28 °C

Variable*	Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Egg to adult	Parameters obtained
Mean ± SE developmental periods of immature stages (in days) of *D. citri*	3.46 ± 0.09	1.57 ± 0.08	1.43 ± 0.08	1.91 ± 0.09	2.29 ± 0.08	3.40 ± 0.09	14.06 ± 0.21	δ_n γ δ_a σ δ_p
% survivorship of immature stages of *D. citri*	96.2	93.4	96.2	99.4	99.1	98.7	83.9	δ_n δ_e

*These values are extracted from tables 1 and 2, respectively, in ref. 6.