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RESEARCH ARTICLE

Developing epidemiological preparedness for a plant disease invasion: Modelling citrus huánglóngbìng in the European Union

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Societal Impact Statement

Huánglóngbìng (HLB) is a bacterial disease of citrus that has significantly impacted Brazil and the United States, although citrus production in the Mediterranean Basin remains unaffected. By developing a mathematical model of spread in Spain, we tested surveillance and control strategies before any future HLB entry in the EU. We found while some citrus production might be maintained by roguing, this requires extensive surveillance and significant chemical control, perhaps also including testing of psyllids (which spread the pathogen) for bacterial DNA. Our work highlights the key importance of early detection (including asymptomatic infection) and vector control for HLB management.

Summary

- Huánglóngbìng (HLB; citrus greening) is the most damaging disease of citrus worldwide. While citrus production in the United States and Brazil have been affected for decades, HLB has not been reported in the European Union (EU). However, a HLB vector, the African citrus psyllid, is already in Portugal and Spain. In 2023, the major vector, the Asian citrus psyllid, was first reported in Cyprus.
- We develop a landscape-scale, epidemiological model, accounting for heterogeneous citrus cultivation and vector dispersal, as well as climate and disease management. We use our model to predict HLB dynamics for an epidemic vectored by the African citrus psyllid in high-density citrus areas in Spain, assessing detection and control strategies.
- Without disease management, we predict large areas infected within 10–20 years. Even with significant visual surveillance, any epidemic will be widespread on first detection, making eradication unlikely. Nevertheless, increased inspection and roguing following first detection, particularly if coupled with intensive insecticide use, could sustain some citriculture for a decade or more, albeit with reduced

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production. However, effective control may require chemical application rates and/or active substances no longer authorised in the EU. Strategies targeting asymptomatic infection will be more successful. Detection of bacteriliferous vectors—sometimes possible long before plants show symptoms—could reduce lags before disease management commences. If detection of HLB-positive vectors were followed by intensive insecticide sprays, this may greatly improve outcomes.

- Our work highlights modelling as a key component of developing epidemiological preparedness for a pathogen invasion that is, at least somewhat, predictable in advance.

KEYWORDS

candidatus Liberibacter, citrus greening, *diaphorina citri* Kuwayama, early detection surveillance, HLB (huánglóngbìng), psyllid, stochastic epidemic model, *trioza erytreae* Del Guercio (1918)

1 | INTRODUCTION

Consequences of plant disease epidemics threaten food security (Strange & Scott, 2005) and ecosystem services (Boyd et al., 2013). Emerging pathogens, which cause disease in new locations or on new plant host species, can be particularly damaging (Ristaino et al., 2021). However, emerging plant disease epidemics are well-documented (Fielder et al., 2024; Jeger et al., 2023; Rosace et al., 2023), and invasion rates are increasing (Bebber et al., 2014). Drivers include changes to farming practices and land use (Anderson et al., 2004), climate change (Singh et al., 2023) and increased travel and trade (Brasier, 2008).

Rising invasion rates have focused attention on how emerging epidemics can be detected and controlled (Cunniffe & Gilligan, 2020). It is particularly important to anticipate and be able to react quickly to invasions, since this gives control the best chance of success (Fraser et al., 2004). But effective surveillance and control strategies can be particularly difficult to devise for invading pathogens because epidemiology in new locations is inadequately characterised (Thompson et al., 2018). Mathematical modelling can play a key role. Models offer a rational basis to integrate what is known with what is not known to design surveillance (Parnell et al., 2017) and to determine when, where and how to control disease (Cunniffe et al., 2015). However, modelling of emerging plant pathogens has very often been done retrospectively (e.g., Cunniffe et al., 2016; Radici et al., 2024).

Here we focus on modelling in advance of an invasion that is, at least somewhat, predictable. We use citrus greening (aka huánglóngbìng, HLB) in the European Union (EU) as a timely and socioeconomically important case study. Worldwide, citrus is the most important fruit crop and HLB is its most devastating disease (Gottwald, 2010). HLB has been reported in over 60 countries (Zhang et al., 2023), and impacts on the citrus industries of Brazil and the United States are extremely significant. For example, since 2005, citrus production in Florida has decreased by 80%, whereas in Brazil over 64 million trees have been removed in São Paulo state alone (Graham et al., 2024). Economic impacts have been correspondingly severe with, for example, estimated impacts upon the citrus industry in the United States of over 3 billion USD per year (Ghosh et al., 2023). However, despite significant and ongoing epidemics elsewhere, HLB has not been reported in the EU, and citrus production in the Mediterranean Basin remains unaffected (Wang, 2020).

HLB is associated with three noncultivable phloem-restricted bacteria: *Candidatus* Liberibacter asiaticus (CLas), *Ca* L. africanus (CLaf) and *Ca* L. americanus (CLam) (Bové, 2006) (throughout this article, when we use the terms “HLB” or “disease”, we may be referring to the pathogens associated with the disease, regardless of the manifestation of symptoms). HLB is primarily transmitted by two insect vectors, the Asian citrus psyllid (ACP), *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) and the African citrus psyllid (AfCP), *Trioza erytreae* Del Guercio (1918) (Hemiptera: Triozidae) (throughout this article, when we use the term “vector”, we may be referring to either of these psyllid species, although as described below we predominantly focus on AfCP). ACP has been found in Asia, North America, South America and a few locations in Africa. There have also been recent detections of ACP in Israel (EPPO (European and Mediterranean Plant Protection Organization), 2022) and Cyprus (EPPO (European and Mediterranean Plant Protection Organization), 2023), although aside from Cyprus, ACP has not been reported in other EU countries. AfCP has been found in many countries in Africa and the Middle East and was reported in Europe in 2014 (Perez-Otero et al., 2015), with subsequent spread over large areas of the Atlantic coast of the Iberian Peninsula (i.e., Spain and Portugal) (EFSA (European Food Safety Authority) et al., 2019). It has been shown experimentally that both ACP and AfCP vector CLas (Reynaud et al., 2022), the most aggressive of the three bacteria causing HLB (Bové, 2006).

Both the recent detections of ACP in Israel and Cyprus and the established presence of AfCP in Spain and Portugal are concerning, since either vector could facilitate HLB transmission were a pathogen to be introduced (Cocuzza et al., 2017). Although contingency plans for the arrival of HLB in Spain and Portugal exist (DGAV (Direção-

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Geral da Alimentação e Veterinária), 2021; BOE (Boletín Oficial del Estado), 2023), and have been tested in formal simulation exercises (Aragón et al., 2022), designing an effective response is challenging. Management interventions that have been used somewhat successfully in other areas might not translate to the EU, since important epidemiological aspects are different. For example, there are differences in how commercial and noncommercial citrus are distributed (Moreira et al., 2019), in climatic drivers of vector population dynamics (Cocuzza et al., 2017), and in regulations dictating which pesticides can be applied and how often (Urbaneja et al., 2020). Each of these factors has knock-on effects upon outbreak management. This is precisely when modelling is most useful.

Here we show how modelling can contribute to developing epidemiological preparedness for a potentially devastating plant pathogen. We have developed a flexible and transferable stochastic landscape-scale model, which accounts for heterogeneity in the citrus host landscape, spatial spread of a vector (including effects of climate and disease management on its population dynamics) and the concomitant spread of HLB. We focus here on the Iberian Peninsula—Spain and Portugal—driven by the availability of citrus density data and the status of Spain as the largest citrus producer in the EU (Schimmenti et al., 2013). However, the fitted model could be applied to any EU region, assuming climatic and citrus host data were available. In Europe, Spain is the main citrus producer, and the country is the sixth largest grower worldwide, with commercial crops covering almost 300,000 ha and producing over 6 million tonnes of fruit per year (MAPA (Ministerio de Agricultura, Pesca y Alimentaciòn), 2023). About 60% of citrus production in Spain is exported. Indeed, Spain is the world's largest exporter of fresh citrus, accounting for about 25% of all exports (FAO (Food and Agriculture Organization), 2021), highlighting the country's influence in the international citrus market (WCO (World Citrus Organization), 2022). Data from the spread of AfCP in Spain and Portugal to date are used to parameterise psyllid dispersal in our model, and this—as well as the presence of AfCP in the region—motivated us to model the case in which pathogen spread is vectored by AfCP. Although both AfCP and ACP are known to transmit HLB (Reynaud et al., 2022), differences in infection rates are not well characterised. Here we made the conservative assumption that ACP and AfCP are equally competent as vectors and that biotic and abiotic conditions are not limiting for vector/pathogen establishment and spread. In part, this is driven by our focus on a worst-case scenario, as would be likely to be necessary in any update to current EU plant health law (EU (European Union), 2016, 2019).

While our model must track spread across large areas of Spain and Portugal when fitting psyllid dispersal parameters, our major focus is to assess and compare surveillance and control strategies before and during the early stage of any epidemic. We do not aim to predict precisely where in the EU the pathogen will enter and so do not attempt to model relative risks of primary infection for different regions (Douma et al., 2016; Rosace et al., 2025). Instead, we concentrate on the situation as faced directly before and after an initial incursion, restricting our attention to two representative 50km × 50km regions in Spain within which commercial citrus is grown at high-density and where HLB and/or AfCP and/or both could be introduced.

We demonstrate how an uncontrolled outbreak might spread if HLB entered, and how the speed of invasion would depend on whether AfCP was already locally widespread. We then investigate early detection surveillance, initially focusing on visual inspection of trees for disease symptoms, testing how the size of any epidemic at the point of first detection responds to the frequency and intensity of surveys. Finally, we assess the effectiveness of strategies for disease control, showing how relative efficacy can be quantified. We also test the potential effects of accelerating early detection, by considering testing vectors for *C*Las DNA via qPCR (Li et al., 2008), and following up first detection with widespread intensive insecticide sprays (over and above the baseline level of disease management, which includes routine insecticide application, as well as regular roguing after first detection). By comparing results for our two representative 50km × 50km regions in Spain, we test the robustness of our conclusions.

2 | DESCRIPTION

2.1 | Modelling spread of vector and disease

2.1.1 | Climatic suitability for the African citrus psyllid

The response of AfCP population density to climate was modelled using daily weather data for Spain and Portugal, obtained from the ERA5-Land dataset (CCDS (Copernicus Climate Data Store), 2019). A day was considered "suitable" for AfCP whenever the vapour-pressure deficit was less than 34.5 mbar and the minimum temperature was greater than 10 °C (Catling, 1973; Paiva et al., 2020). The climate suitability, w_i (Figure 1a)—which affects local vector population density in our model (see below)—was then simply the proportion of days with suitable conditions taken over the entire 2009 to 2018 period.

2.1.2 | Citrus host distribution

Commercial and residential/municipal (henceforth "residential") citrus were mapped across Spain and Portugal, and rasterised at 1km × 1km resolution (Figure 1b; see also Supporting Information Methods S1). Our mapping also divides commercial citrus into subcategories: typical (actively cultivated, with insecticides sprayed), abandoned (not cultivated) and organic (only cultural and/or biological control). These three subcategories are amalgamated within commercial citrus when modelling spread, but effects on vector density are accounted for when modelling pest management by insecticide (see below). Planting densities of commercial citrus vary, sometimes quite widely, depending on citrus species/variety, soil type and other agronomic factors. However, a reasonable estimate of average citrus

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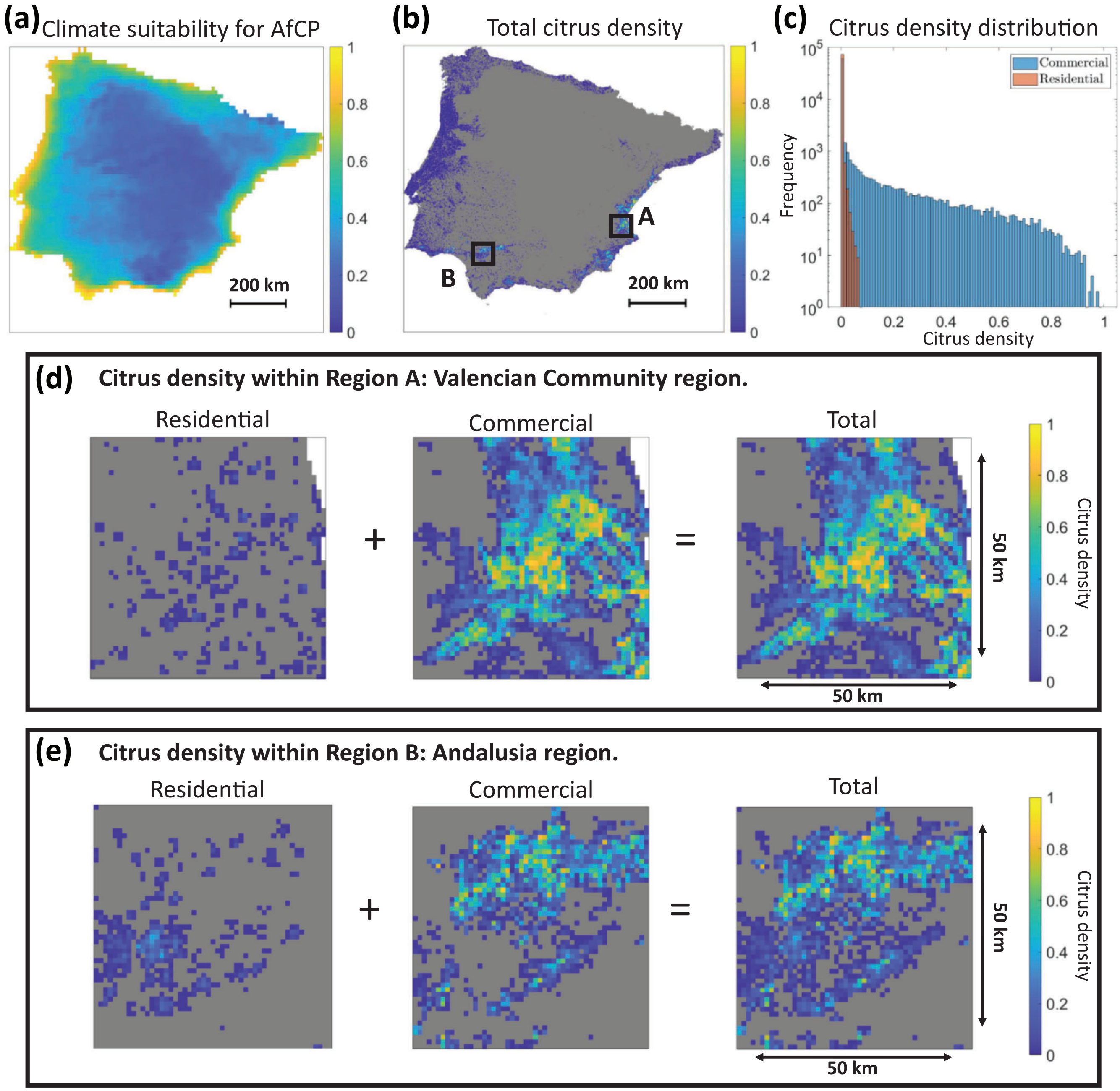

FIGURE 1 Climate suitability and citrus density across the Iberian peninsula. (a) Climatic suitability for AfCP (African Citrus Psyllid). (b) Total citrus density (residential + commercial) for each 1 km × 1 km cell, with our two 50 km × 50 km focal regions labelled. A tree density of 1.0 corresponds to around 50,000 trees per km^2 (see main text). (c) Frequency distributions of (nonzero) residential and commercial citrus densities in each cell. (d) Residential, commercial and total citrus density maps (Region A), within the Valencian Community region, on the east coast of Spain. (e) Residential, commercial and total citrus density maps (Region B), within Andalusia, in southern Spain.

densities in Spanish citriculture is around 500 trees per hectare (Agustí et al., 2020), meaning that a density of $h_i^c = 1.0$ corresponds to around 50,000 trees per km^2.

For cell i, citrus densities (h_i^c and h_i^r; see also Table 1) were converted into pairs of integer-valued numbers of "host units" ($0 \leq H_i^c \leq 100$ and $0 \leq H_i^r \leq 1{,}000$) for compatibility with our epidemiological model. Each commercial host unit therefore corresponds to an area of 100 m × 100 m (1 ha), whereas each residential host unit corresponds to an area of approximately 32 m × 32 m (0.1 ha). We used different discretisations for commercial and residential citrus to allow our model to properly capture within-cell epidemiological dynamics, since within-cell densities are rather different (Figure 1c), largely because commercial trees are typically planted in rows of hundreds/thousands of trees in close proximity. The largest number of residential host units in any cell across the whole of Spain and Portugal was in fact 71 (out of a potential maximum of 1000),

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TABLE 1 State variables/symbols for host/vector densities and infestation/infection status of citrus in cell *i*.

Symbol	Meaning	Range
$h_i^{\{r,c\}}$	Density of citrus (in km^2 per km^2 cell)	0–1
$H_i^{\{r,c\}}$	Number of citrus "host units"	0–$N_{max}^{\{r,c\}}$
$S_i^{\{r,c\}}$	Number of susceptible (i.e., uninfected) host units	0–$H_i^{\{r,c\}}$
$E_i^{\{r,c\}}$	Number of exposed (i.e., uninfectious/asymptomatic) host units	0–$H_i^{\{r,c\}}$
$C_i^{\{r,c\}}$	Number of cryptic (i.e., infectious/asymptomatic) host units	0–$H_i^{\{r,c\}}$
$I_i^{\{r,c\}}$	Number of infected (i.e., infectious/symptomatic) host units	0–$H_i^{\{r,c\}}$
$R_i^{\{r,c\}}$	Number of removed (i.e., rogued) host units	0–$H_i^{\{r,c\}}$
$X_i^{\{r,c\}}$	Psyllid absent (i.e., psyllid has not infested)	0 or 1
$Y_i^{\{r,c\}}$	Psyllid exposed (i.e., psyllid present, but has not yet fully colonised)	0 or 1
$Z_i^{\{r,c\}}$	Psyllid infested (i.e., psyllid fully colonised and can disperse elsewhere)	0 or 1
$V_i^{\{r,c\}}$	Relative density of colonising psyllids from cell *i* (see also Equation 1)	0–1

Note: All symbols are superscripted with either *r* or *c*, depending on whether commercial or residential citrus is considered. The maximum number of host units in a single cell differs between residential and commercial citrus, with $N_{max}^r = 1000$ and $N_{max}^c = 100$. As described in Methods, this is to allow the model to have sufficient resolution to track within-cell HLB (huánglóngbìng) infection dynamics in both types of citrus. State variables for psyllid infestation status are indicator variables, with $X_i^{\{r,c\}} + Y_i^{\{r,c\}} + Z_i^{\{r,c\}} = 1$ (i.e., citrus of each type can be in one and only one of the three distinct classes), and $V_i^{\{r,c\}} > 0$ only if $Z_i^{\{r,c\}} = 1$, i.e., psyllids can only disperse (and, if relevant, transmit infection) from fully colonised cells (see also Equation (1)).

corresponding to a 1 km × 1 km (i.e., 100 ha) cell with 7.1 ha of trees (in residential settings). If the discretisation adopted for commercial citrus were used unchanged for residential citrus, then the number of residential host units would almost always be very small (and would always be ≤ 7). The model therefore would not have very much resolution within the relevant range of citrus densities to represent within-cell increases in local infection as the residential citrus within any cell became progressively more infected.

2.1.3 | Bacterium and vector

We focus on the CLas bacterium as it is the most damaging, as well as the most likely to be introduced due to large and ongoing epidemics worldwide (Gottwald, 2010). We focus on AfCP as the vector, motivated by the availability of psyllid spread data from the recent invasion of the Atlantic coast of the Iberian Peninsula (Cocuzza et al., 2017), and concomitant risk of spread of AfCP to regions of the Iberian Peninsula with commercial citriculture.

2.1.4 | Disease and vector status within each cell

Our model tracks the HLB status of each citrus host unit in each cell, for both residential and commercial citrus. We distinguish the following: (*S*)usceptible, (*E*)xposed, (*C*)ryptic, (*I*)nfected and (*R*)emoved (Figure 2). Susceptible host units are uninfected. Exposed host units are latently infected, that is, not yet infectious. Cryptic host units are infectious but not yet symptomatic (Craig et al., 2018). Infected host units are infectious and symptomatic. Removed host units have been rogued (i.e., removed following detection to slow or stop the spread of disease). We do not account for other citrus demography, for example, planting or disease-induced/natural death.

Epidemiological transitions of host units—and all other events in the Matlab (version 9.13.0 (R2022b) The MathWorks Inc. 2022) implementation of our stochastic model—are simulated using Gillespie's algorithm (Keeling & Rohani, 2008). Transitions from $E \to C$ and $C \to I$ occur at fixed rates μ and ν, respectively, with average latent period of 1 year and average incubation period (i.e., to detectable symptoms) of 1.25 years (Parry et al., 2014) (Table 2). The rate at which host units transition from $S \to E, \lambda$, is complex and depends on psyllid dispersal and the infection status of citrus within the cell of interest and elsewhere, as described below. The transition from $I \to R$ occurs at rate ω and depends on the detection and control strategy adopted, since it corresponds to roguing.

AfCP is currently only present along the Atlantic coast of the Iberian Peninsula, and so we model whether each cell's citrus is infested by the psyllid. The model tracks whether cells are colonised by populations of psyllids that are sufficiently well-established for dispersal elsewhere, distinguishing infestation statuses of residential and commercial citrus. For each class of citrus, in each cell, there are three possibilities: vector absent (*X*), exposed (*Y*) and infested (*Z*) (see also Table 1). Exposed corresponds to a recently arrived vector population which is not yet capable of further dispersal. The rate of the $X \to Y$ transition, γ, is complex and is described below. We assume the rate of the $Y \to Z$ transition is $\eta = 1$ yr^{-1}, corresponding to an average of one year for psyllid populations to fully colonise cells (see Parameterisation, below).

Following colonisation, relative psyllid population densities in cell i, V_i^r and V_i^c, depend on local citrus densities and environmental conditions

$$V_i^r = h_i^r w_i Z_i^r, \quad \text{and} \quad V_i^c = h_i^c w_i m_i Z_i^c, \tag{1}$$

where h_i^r and h_i^c are proportions of residential/commercial citrus ($0 \le h_i^r, h_i^c \le 1$) and w_i is the climate suitability for psyllids ($0 \le w_i \le 1$). For commercial citrus, the effect of pest management, m_i is also included ($0 \le m_i \le 1$; see also Supporting Information Methods S1 and note our mapping procedure allows us to account for a lack of insecticide sprays in abandoned and/or organic orchards). In Equation (1), the infestation status (i.e., Z_i^r or Z_i^c) acts as an indicator function to ensure psyllid densities are only nonzero when the cell is fully colonised.

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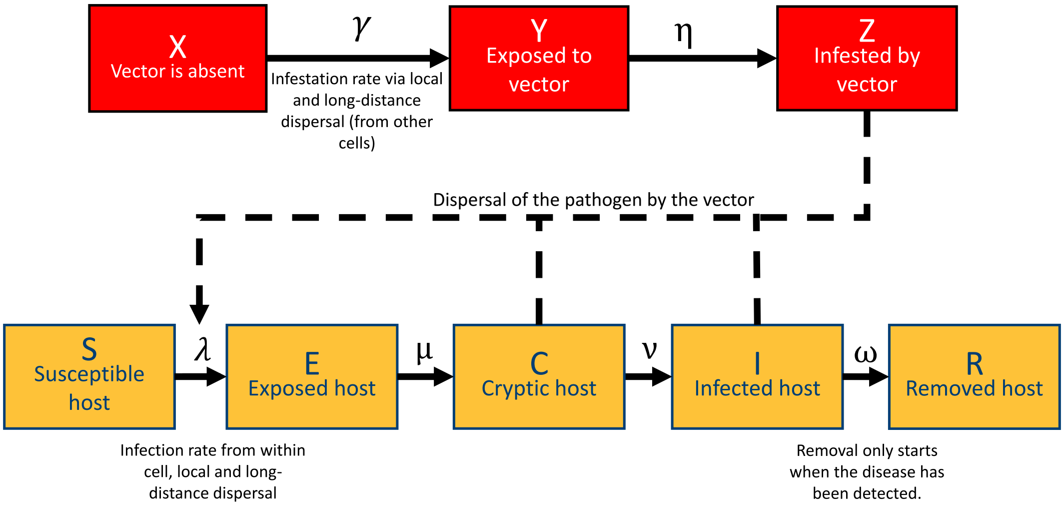

FIGURE 2 Model of vector (AfCP; African Citrus Psyllid) and pathogen (CLas; *Candidatus* Liberibacter asiaticus) in each 1km × 1km cell. We track each cell's vector infestation status, for each class of citrus (residential/commercial), distinguishing: free of vector, X, exposed (psyllid is present but has not yet fully colonised the cell), Y, and infested, Z. We also track the disease status of citrus within each cell, quantifying local densities of infection by tracking the number of host units in each epidemiological class in each cell, again distinguishing residential from commercial citrus. Epidemiological classes: susceptible (free from HLB), S; exposed (latently infected), E; cryptic (infectious but not symptomatic), C; infected (infectious and symptomatic), I; and removed, R (controlled by roguing). The rate from $X \rightarrow Y, \gamma$, is the combination of local and long-distance dispersal of the vector (Γ, Equations (2) and (3) and Ω, Equation 4). The rate from $S \rightarrow E, \lambda$, is the equivalent combination for infection (Λ, Equations (5) and (6), and Ω, Equation (4)).

TABLE 2 Model parameters, descriptions, values and sources.

Parameter		Estimate and source	
δ	Psyllid dispersal rate	1,600 d^{-1}	Fitted (see text)
ζ	Proportion of long-distance dispersal	0.001	Fitted (see text)
α_{loc}	Local dispersal scale	1.96 km	Nguyen et al. (2023)
α_{ld}	Long-distance dispersal scale	130 km	Benhadi-Marín et al. (2020)
m	Vector reduction in commercial citrus	0.9	Qureshi et al. (2014)
η	Rate of vector establishment	1/365 d^{-1}	Assumed/fitted (see text)
β	Infection rate	10d^{-1}	Fitted (see text)
ρ	Proportion of within cell infection	0.7	Fitted (see text)
μ	Exposed to cryptic transition rate	1/365 d^{-1}	Parry et al. (2014)
ν	Cryptic to symptomatic transition rate	5/365 d^{-1}	Parry et al. (2014)
ω	Roguing rate	0	No control by default

Note: Model fitting is described in overview in the main text, with further details in Supporting Information Methods S3.

2.1.5 | Interactions between cells

Scales of dispersal

We distinguish two scales of dispersal. The local dispersal kernel, K_{ij}^{loc}, reflects psyllid movement between an individual cell, i, and one of its near neighbours, j. For this, we use an exponential kernel as fitted to spread of ACP in the United States by Nguyen et al. (2023). However, psyllids can occasionally travel much further, due to extreme wind (Antolinez et al., 2021) or human transportation (Nunes et al., 2023). We capture these relatively infrequent long-distance dispersals using t-distribution kernel as fitted to the AfCP invasion in Portugal by Benhadi-Marín et al. (2020). Mathematical details are in Supporting Information Methods S2).

Dispersal of psyllids

Local dispersal of psyllids (AfCP) occurs from populations which have colonised neighbouring cells, with local forces of infestation on cell i

$$\Gamma_i^r = \underbrace{1_{\left(H_i^r > 0 X_i^r = 1\right)}}_{\substack{\text{Cell } i \text{ has}\\ \text{uninfested citrus}\\ \text{of class } r}} \overbrace{\delta(1-\zeta)}^{\substack{\text{Rate of local}\\ \text{dispersal}}} \underbrace{w_i}_{\text{Climate}} \overbrace{\sum_j}^{\substack{\text{Sum}\\ \text{over } j}} \underbrace{K_{ij}^{loc}}_{\substack{\text{Dispersal}\\ j \rightarrow i}} \overbrace{\left(V_j^r + V_j^c\right)}^{\substack{\text{Vectors}\\ \text{in cell } j}}, \tag{2}$$

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and

$$\Gamma_i^c = \overbrace{1_{(H_i^c>0X_i^c=1)}}^{\text{Cell } i \text{ has uninfested citrus of class } c} \underbrace{\delta(1-\zeta)}_{\text{Rate of local dispersal}} \overbrace{w_i}^{\text{Climate}} \underbrace{m_i}_{\text{Management}} \overbrace{\sum_j}^{\text{Sum over } j} \underbrace{K_{ij}^{loc}}_{\text{Dispersal } j\to i} \overbrace{\left(V_j^r+V_j^c\right)}^{\text{Vectors in cell } j}, \tag{3}$$

where $H_i^r, H_i^c > 0$ and $X_i^r, X_i^c = 1$ ensure that only cells containing citrus but currently psyllid-free can become infested, V_j^r and V_j^c are densities of (established) psyllid populations in residential/commercial citrus in cell j, K_{ij}^{loc} is the local dispersal kernel, δ is the rate of psyllid dispersal and ζ is the proportion of long-distance dispersals. For both residential and commercial citrus, forces of infestation include w_i, representing climatic effects. For commercial citrus, m_i is also included in Equation (3), representing reduced establishment probability due to pest management (i.e., insecticide sprays).

Our model implements the "particle-emission" formulation of long-distance dispersal (Meentemeyer et al., 2011). Rates of long-distance dispersal from cell i are

$$\Omega_i^r = \delta\zeta V_i^r \text{ and } \Omega_i^c = \delta\zeta V_i^c, \tag{4}$$

where δ is the dispersal rate, ζ is the proportion of long-distance dispersals and V_i^r and V_i^c are densities of psyllid populations in residential/commercial citrus in cell i. Whenever a long-distance dispersal event is sampled by our Gillespie algorithm, the angle of dispersal is drawn uniformly on $[0,2\pi)$ and a distance sampled from the long-distance dispersal kernel. If the corresponding destination cell, j, contains citrus, the type of citrus challenged (residential or commercial) is randomly chosen according to the proportion of each type. The probability the vector will infest is given by w_j for residential citrus, or $w_j m_j$ for commercial citrus. If cell j does not contain citrus, the vector simply fails to disperse.

Spread of infection.

Infection rates are closely coupled to psyllid dispersal. However, since our model captures HLB dynamics within individual cells, within- and between-cell infection must be distinguished. The rate of local infection of susceptible host units in residential citrus in cell i (i.e., the component of the rate of the $S \to E$ transition in cell i corresponding to within-cell and nearby sources of infection) is

$$\Lambda_i^r = \underbrace{1_{(H_i^r>0)}}_{\text{Cell } i \text{ has citrus of class } r} \overbrace{\beta}^{\text{Infection rate}} \underbrace{\frac{S_i^r}{H_i^r}}_{\text{Proportion that is uninfected}} \left[\overbrace{\rho\left(J_i^r V_i^r + J_i^c V_i^c\right)}^{\text{Within-cell infection}} + \underbrace{(1-\rho)\sum_{j,j\neq i} K_{ij}^{loc}\left(J_j^r V_j^r + J_j^c V_j^c\right)}_{\text{Between-cell infection (accounts for local dispersal)}}\right], \tag{5}$$

and for commercial host units is

$$\Lambda_i^c = \underbrace{1_{(H_i^c>0)}}_{\text{Cell } i \text{ has citrus of class } c} \overbrace{\beta}^{\text{Infection rate}} \underbrace{\frac{S_i^c}{H_i^c}}_{\text{Proportion that is uninfected}} \left[\overbrace{\rho\left(J_i^r V_i^r + J_i^c V_i^c\right)}^{\text{Within-cell infection}} + \underbrace{(1-\rho)\sum_{j,j\neq i} K_{ij}^{loc}\left(J_j^r V_j^r + J_j^c V_j^c\right)}_{\text{Between-cell infection (accounts for local dispersal)}}\right]. \tag{6}$$

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In Equations (5) and (6), β is the infection rate, S_i^c/H_i^c and S_i^r/H_i^r are proportions of uninfected commercial/residential host units in cell i, ρ is the proportion of within-cell transmission and J_j^c and J_j^r are proportions of infectious commercial/residential citrus in cell j, i.e.,

$$J_j^r = (I_j^r + C_j^r)/H_j^r, \text{ and } J_j^c = (I_j^c + C_j^c)/H_j^c. \tag{7}$$

Long-distance transmission of HLB is a consequence of psyllid movement. Whenever long-distance psyllid dispersal occurs from residential citrus in cell i, the probability the recipient cell (j) gains a single HLB exposed host unit is given by $J_i^r(S_j^r/H_j^r)$ or $J_i^r(S_j^c/H_j^c)$, depending on whether the long-distance dispersal challenges residential or commercial citrus. Analogous probabilities involving J_i^c set the chance of infection from long-distance dispersal from cell i originating within commercial citrus. There is no requirement for a vector population to establish in the recipient location for transmission of the bacterium, and so parameters for climate and pest management are not included in these probabilities. However, of course, infection will not be able to spread onwards from any infected cell until a psyllid population does colonise locally.

2.1.6 | Parameterisation

We fix values of five parameters in our model from the literature (Table 2): α_{loc} (scale of local psyllid dispersal); α_{ld} (scale of long-distance psyllid dispersal); m (effect of insecticide sprays on psyllid populations); μ (rate at which exposed hosts become cryptic); and ν (rate at which cryptic hosts become symptomatic). The rate of roguing, ω, depends on the control strategy, and in model runs without disease control, we assume $\omega = 0$.

However, five remaining parameters are fitted to data (Supporting Information Methods S3). These are the following: δ (dispersal rate of psyllids), ζ (proportion of long-distance psyllid dispersal), η (rate at which psyllids fully colonise a cell following first infestation), β (pathogen transmission rate) and ρ (rate of within-cell relative to between-cell infection). Parameters δ and ζ are fitted to AfCP presence data from surveys in Portugal and Spain up to 2021 (Benhadi-Marín et al., 2022), contingent on an assumed value of η. To fit parameters β and ρ, we calibrated results our model against a previous model of the spread of HLB (*C*Las vectored by ACP) in Florida (Mastin et al., 2020). Full details are in Supporting Information Methods S3.

2.2 | Modelling detection and control

2.2.1 | Early detection

Before first detection, we model regular surveys every Δ ("inspection interval") years, with a^c% and a^r% of cells containing commercial and residential citrus, respectively, across our 50km × 50km region, randomly selected on each round of inspection. Selection is weighted by within-cell citrus density. Within each selected cell, at any inspection, n_h host units are selected at random (if the cell has fewer than n_h host units of the prescribed type, all are inspected). Disease is detected by visual inspection of trees for disease symptoms with probability p on each symptomatic (i.e., class I) host unit. The first inspection is at a random time on $[0, \Delta)$, where 0 is the time of first introduction.

2.2.2 | Control

Following first detection, we assume surveillance significantly intensifies, occurring according to the roguing interval, Δ_R (generally with $\Delta_R < \Delta$). This detection regime applies across the region, and so we assume that the entire 50km × 50km area corresponds to the Infested Zone under Regulation (EU) 2016/2031 (EU (European Union), 2016). We assume that the increased threat of disease encourages most stakeholders to participate in enhanced detection and control. However, since some growers will not cooperate, we introduce a compliance parameter, c, and assume only a proportion c of growers comply. The set of noncomplying growers remains fixed for each simulation. We assume that detection and control does not occur within the cells containing non-compliant growers. However, we assume that all host units in all complying cells are inspected on each roguing interval.

Detection of symptomatic host unit(s) triggers roguing (i.e., removal of host). Following detection, which as for early detection occurs with probability p for symptomatic host units, each detected host unit is (immediately) removed with probability q. With probability $1 - q$, a host unit will not be removed, although of course it may be re-detected and removed later. The roguing probability, q, therefore acts as a proxy for any delays in control and/or imperfect management by growers or plant health authorities. We also allow for commercial growers applying extra pest management following first detection. This reduces the vector population by a further factor m^*, over-and-above the reduction by m caused by "standard" pest management. We model this by assuming m is increased by $(1 - m)m^*$ across the entire region of interest immediately after first detection and that this decreases vector populations in commercial citrus (while accounting for abandoned/organic citrus, and only for the subset of growers who comply).

2.2.3 | Parameterisation

Since *C*Las is an EU priority pest (EU (European Union), 2016, 2019), annual surveys are mandatory, and so inspection is assumed once per year ($\Delta = 1$yr). We assume by default (see also Table 3) $a^c = 1$% of cells with commercial citrus are (randomly) surveyed each year, and within each cell $n_h = 5$ (commercial), host units are inspected. However, by default, residential citrus is not inspected ($a^r = 0$%), reflecting the difficulty of surveillance in private

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TABLE 3 Default parameters for detection and control strategies.

Parameter		Value
Early detection		
Δ	Inspection interval	1 years
a^c	Percentage of commercial cells surveyed	1%
a^r	Percentage of residential cells surveyed	0%
b^c	Percentage of commercial cells surveyed for CLas positive psyllids	0%
b^r	Percentage of residential cells surveyed for CLas positive psyllids	0%
n_h	Number of host units sampled per surveyed cell	5
p	Probability of detection of symptomatic host units	0.5
p_v	Probability of detection of CLas positive psyllids	0.9
Control following first detection		
Δ_R	Roguing interval	0.5 years
a^c	Percentage of commercial cells surveyed	100%
a^r	Percentage of residential cells surveyed	0%
n_h	Number of host units sampled per surveyed cell	100
p	Probability of detection of symptomatic host units	0.5
c	Proportion of stakeholders who comply with control	0.9
q	Roguing probability	0.9
m^*	Effectiveness of additional spraying by commercial growers	0

Note: There is initially an early detection phase, but following detection anywhere across the region, the strategy switches to include more intensive surveillance and active disease control (details in text).

gardens and other residential settings (Cocuzza et al., 2017). We assume that the probability of (visual) detection of symptomatic hosts is $p = 0.5$ (Mastin et al., 2020).

After detection of the pathogen anywhere within the region, our baseline is that the default compliance rate of commercial growers is 90% (i.e., $c = 0.9$). For those growers who comply, the roguing interval is $\Delta_R = 0.5$ (i.e., detection/control every 6 months) and all commercial citrus units are inspected within all cells ($n_h = 100, a^c = 100\%$). The roguing probability is $q = 0.9$. However, we assume that residential citrus remains uninspected ($a_R^c = 0\%$); because of this, by default, we assume no roguing is done for residential citrus. We also assume that there is no additional pest management introduced by commercial growers (i.e., $m^* = 0$). However, our sensitivity analyses allow consequences of these choices to be tested.

2.2.4 | Testing vectors for CLas DNA as an early warning system

Our model tracks the HLB infection status of citrus host units rather than individual trees and does not include the population dynamics or infection status of psyllids at subcellular levels. We therefore do not attempt to model the fine details of detection on psyllids and instead use a phenomenological model. We assume that psyllids (if any are present) in $b^r\%$ and $b^c\%$ of residential and commercial cells, respectively, are annually sampled and tested for CLas DNA. Furthermore, we assume that a sufficient number of psyllids is tested such that any local HLB infection—irrespective of its local density or symptom status—will be found with probability, p_v. Within each cell tested, detection therefore occurs according to a single Bernoulli trial, with probability of success

$$\mathbb{P}(\text{Detect}|\text{Sample cell } i) = \overbrace{\mathbb{1}_{(Y_i^c + Z_i^c + Y_i^r + Z_i^r > 0)}}^{\text{Cell } i \text{ has psyllids}} \underbrace{\mathbb{1}_{(E_i^c + C_i^c + I_i^c + E_i^r + C_i^r + I_i^r > 0)}}_{\text{Cell } i \text{ has infection}} p_v, \quad (8)$$

where $p_v \in [0,1]$ is a proxy for the sampling sensitivity and number of psyllids tested per cell.

We focus on testing for CLas DNA to permit early detection, taking detection of bacterialiferous psyllids as an early warning signal of pathogen invasion. Before the pathogen is detected anywhere in the 50 km × 50 km region of interest, we assume the host is no longer sampled (i.e., $a^c = a^r = 0$). However, psyllids from 1% of all cells containing commercial citrus are subjected to annual sampling (i.e., $b^c = 1\%$), with probability of detection of CLas positive psyllids given any infection is present taken to be $p_v = 0.9$. Following first detection, we revert to the "Control" scenario described above, with six-monthly visual inspection of hosts for HLB symptoms, and roguing of commercial citrus. However, we assume that control also involves additional insecticide sprays in all commercial citrus, first applied immediately after the time of detection, at rate of application sufficient to provide an extra management effectiveness of 50% (i.e., $m^* = 0.5$). We also present a sensitivity analysis to these choices.

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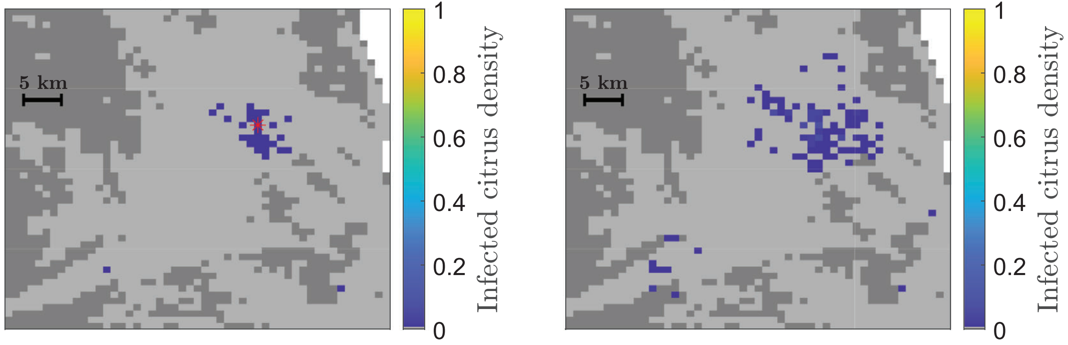
3 | RESULTS

3.1 | Disease spread without control

We initially focus on Region A (Figure 1d), in the Valencian Community region (eastern Spain), one of the main citrus growing regions in the EU. In the absence of the pathogen, the vector is able to spread throughout the region very rapidly (Supporting Information Figure S1 and Movie S1). If both the vector and the pathogen are introduced simultaneously into a single cell, the pathogen also spreads rapidly (Figure 3 and Supporting Information Movie S2), although—of course—slightly slower than the vector in isolation. In the exemplar simulation we consider, several cells near to the point of initial introduction and two cells which are further away become HLB positive within the first year (Figure 3a). Almost all cells with citrus have at least one infected citrus host unit by year 10 (Figure 3(D)), and within

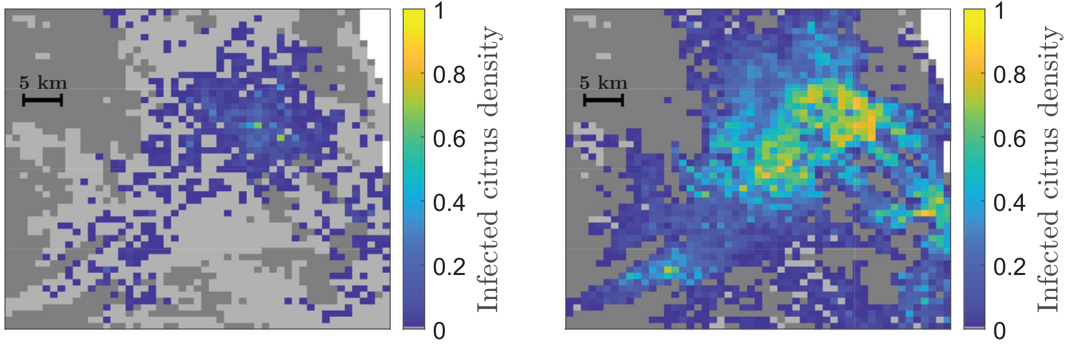
(a) Year 1

(b) Year 2



(c) Year 5

(d) Year 10



(e) Year 20

(f) Citrus infection status

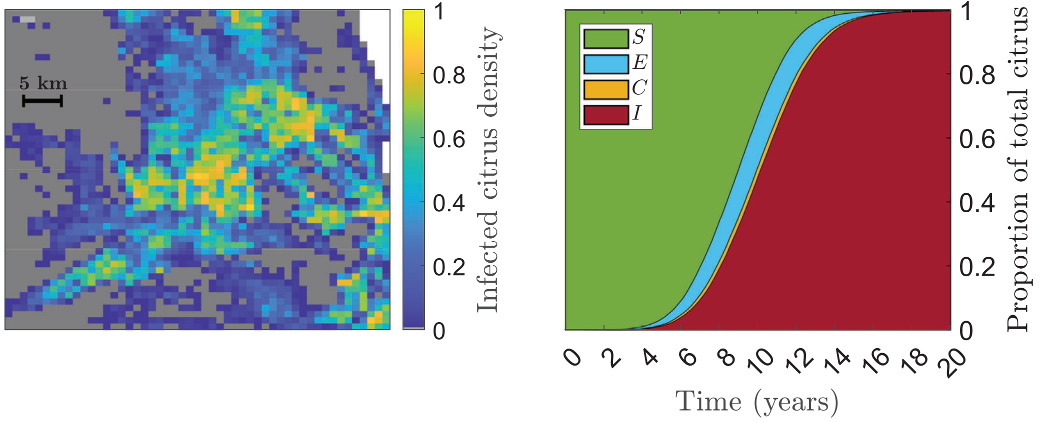


FIGURE 3 Spread of disease in a single simulation in Region A (Valencia). Both vector and pathogen are introduced simultaneously at $t = 0$ into a single $1\text{km} \times 1\text{km}$ cell (asterisked in panel (a)). A single host unit of commercial citrus is moved from $S \rightarrow E$, and the psyllid status of commercial citrus in that cell set to Y. (a–e) Maps showing the density of infected citrus host units $(E + C + I)$ within each cell at different times after introduction; see also Supporting Information Movie S2. (f) Disease progress curve showing proportions of citrus over the entire region in each epidemiological compartment, (S)usceptible, (E)xposed, (C)ryptic and (I)nfected (no host units are (R)emoved, since disease control by roguing was not done in the underpinning simulation).

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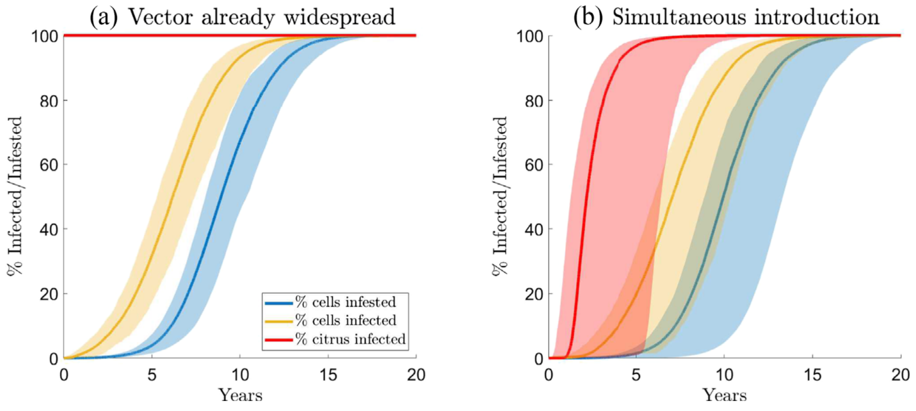

FIGURE 4 Effect of prior invasion by the vector on disease spread in Region A (Valencia). The percentage of cells infested by the vector (red), with at least one infected unit of citrus (yellow) and the percentage of all citrus infected (blue), when the vector is already widespread throughout the region of interest (Panel (a)) *versus* when the vector and pathogen are introduced simultaneously (Panel (b)). In all cases, the pathogen is introduced into the same cell at $t = 0$; for the simulations shown in Panel (b), the cell initially infested by the vector is chosen at random from all cells containing commercial citrus. Shaded regions show 95% prediction intervals from an ensemble of 200 simulation results.

20 years, almost all susceptible citrus across the entire region is infected (compare Figure 3e with Figure 1d).

Although individual simulations are easy to visualise, only ensembles of multiple simulations capture the range of possibilities from our stochastic model. Although the vector spreads rapidly, and it does not take long for an initial vector population to become widely dispersed, if the vector is already widespread at the time of pathogen entry, HLB invasion is faster, since spread can begin immediately (compare Figure 4a,b). Prediction intervals are wider when the vector must also spread, since the variability in the spread of the vector has a knock-on effect upon HLB. This is particularly pronounced when the vector is (randomly) introduced into a cell with low density citrus.

Henceforth, we focus exclusively on the case in which the vector is already widespread in the region of interest. However, in all subsequent simulations, the initial location of CLas infection is selected at random (weighted by commercial citrus density, assuming that the pathogen is introduced on planting material and that higher density commercial operations plant larger amounts more frequently).

3.2 | Early detection surveillance

We test early detection surveillance by varying the proportion of commercial cells inspected on each survey (a^c) and the interval between successive surveys (Δ), considering three indicative probabilities of detection: $p = 0.2, 0.5$ and 0.8. We vary a^c from 0.5% (9 cells across Region A) to 5% (83 cells). We vary the inspection interval (Δ) from once every 3 months to once every 2 years. The number of host units of citrus to inspect per cell is fixed at the default value $n_h = 5$ (this is relaxed in Supporting Information Figure S2).

We summarise performance via the time until first detection and proportion of citrus then infected (Figure 5). Unsurprisingly, effective early detection is conditioned on inspecting as many cells as possible, as often as possible (Figure 5a,d). However, we note that the variability in both time of first detection (Figure 5b,e and [particularly] the proportion of citrus infected (Figure 5c,f) is larger when the probability of detection, p is lower. There are limited returns from increasing the probability of detection if that probability is already relatively high (compare larger differences between responses for $p = 0.2$ and $p = 0.5$ to smaller differences between those for $p = 0.5$ and $p = 0.8$ in Figure 5b,c,e,f).

3.3 | Effectiveness of control

3.3.1 | Default parameterisation

We examine first a single simulation using the baseline strategy (Table 3), in which early detection surveillance is followed by more intensive detection and control once the pathogen is detected (Figure 6 and Supporting Information Movie S3), noting that results in this single simulation are typical of those from a much larger ensemble (see also Supporting Information Figure S3). Although roguing—which in this particular simulation started following detection around 5 years after first introduction—slows disease spread (compare Figures 3 and 6), after 20 years, 65% of all citrus host units have been removed, a further 12% of units are infected and the epidemic is still ongoing, although spreading relatively slowly. Cells containing high densities of infected citrus (green/yellow cells in Figure 6e) are those within which commercial growers are noncompliant and so from which no infected citrus is removed. Such uncontrolled locations act as a source of inoculum driving the ongoing epidemic.

3.3.2 | Sensitivity analysis

We do a series of one-way sensitivity scans, examining percentages of infected/removed citrus over time when varying single parameters

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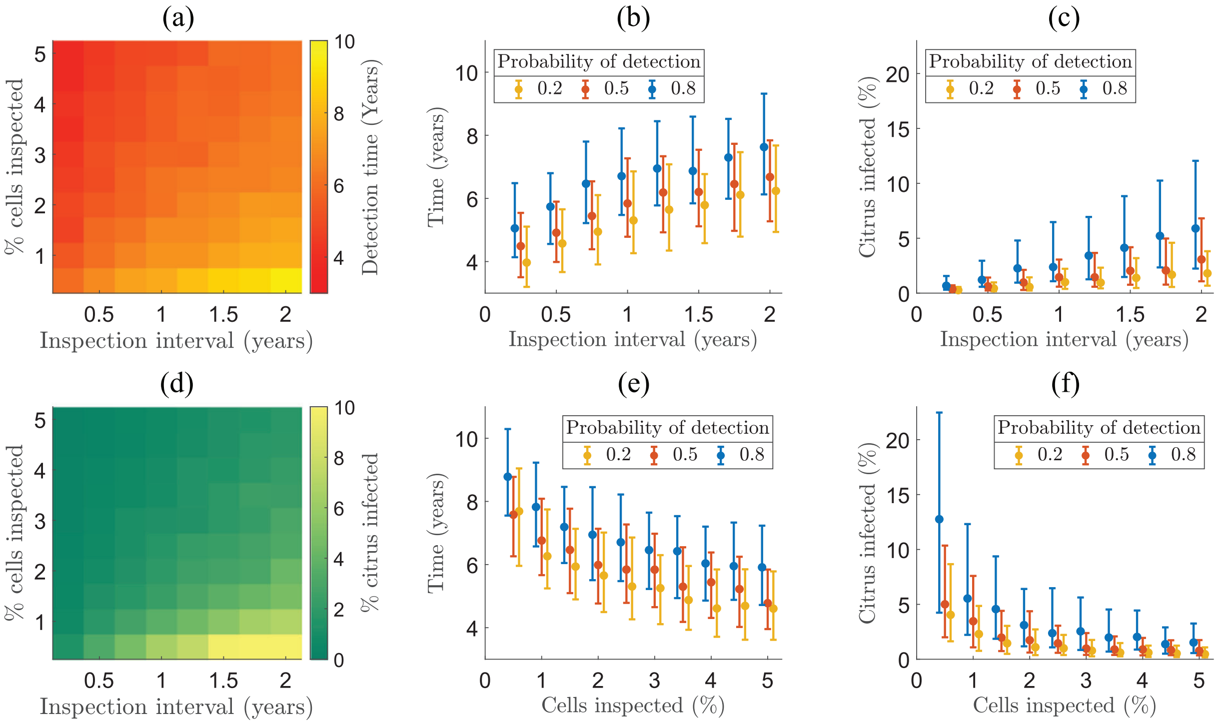

FIGURE 5 Effectiveness of surveillance strategies in Region A (Valencia). (a) Mean time of detection and (d) Mean percentage of total citrus infected at the time of detection. The number of host units sampled in each surveyed cell is $n_h = 5$ and the probability of detection of symptomatic host units is $p = 0.5$. (b,c,e,f) Median and interquartile ranges of (b,e) time until detection and (c,f) proportion of citrus that is infected. The inspection interval and percentage of cells inspected are varied; (b,c) has fixed 5% of cells inspected at varying intervals, and (e,f) varies the percentage of cells inspected at a fixed 12-month inspection interval. Plots show responses for three values of the probability of detection, $p = 0.2, 0.5$ and 0.8. Results are shown from ensembles of 200 simulations for each set of parameters.

in ensembles of simulations (Figure 7). These scans conveniently summarise the relative importance of different aspects of disease management. Reducing the roguing interval (Δ_R) and the compliance and roguing parameters (c and q) have strong effects on the epidemic (Figure 7a,b,e), as these parameters directly impact the rate and/or number of units of citrus removed. Conversely, the proportion of cells inspected in the early detection strategy (a^c) does not have a substantial effect on epidemic rates (Figure 7f), since it only affects the time of first detection. Roguing commercial citrus is essential (Figure 7c), since the vast majority of citrus is commercial, although additional management of residential/municipal citrus leads to a visible difference in epidemic progression.

However, the parameter with the strongest impact on control effectiveness is m^*; the effectiveness of additional pest management to reduce the size of the vector population once the pathogen is detected (Figure 7d). Even before detection, we assume that routine insecticide sprays lead to a $m = 90\%$ reduction to vector densities in commercial citrus. However, if HLB detection triggers additional pest management, and if the psyllid population is reduced by up to 99%, this can slow the progression of the epidemic, although it does not stop spread completely. We return to the plausibility of such high levels of vector control in the EU below. We also note that relative efficacies of different management strategies are unaffected by prior invasion of the vector (Supporting Information Figure S4).

3.3.3 | Robustness

We repeat our analysis of control efficacy for Region B (Figure 1e), in the Andalusia region (southwestern Spain). Region B has less high-density commercial citrus than Region A, although still contains substantial production, and more residential citrus that may hinder attempts to control spread. Region B is also much closer to where AfCP has already been found, and so may be at higher risk. However, since Region B is further inland, there is a lower climate suitability compared to Region A. Figure 8 shows the importance of each parameter, equivalent to Figure 7 for Region A (further results for Region B are in Supporting Information Figures S5–S9 and Movies S4–S6). Impacts of control measures are remarkably similar between the two regions, and additional pest management (m^*) remains the most effective intervention.

3.3.4 | Testing vectors for CLas DNA as an early warning system

We perform a series of sensitivity scans to parameters affecting the efficiency of the potential early warning system provided by testing vectors for CLas DNA (Figure 9). We vary the proportion of cells within which psyllids are tested (b^c), the probability of detecting positive psyllids if any infection is present (p_v) and the additional

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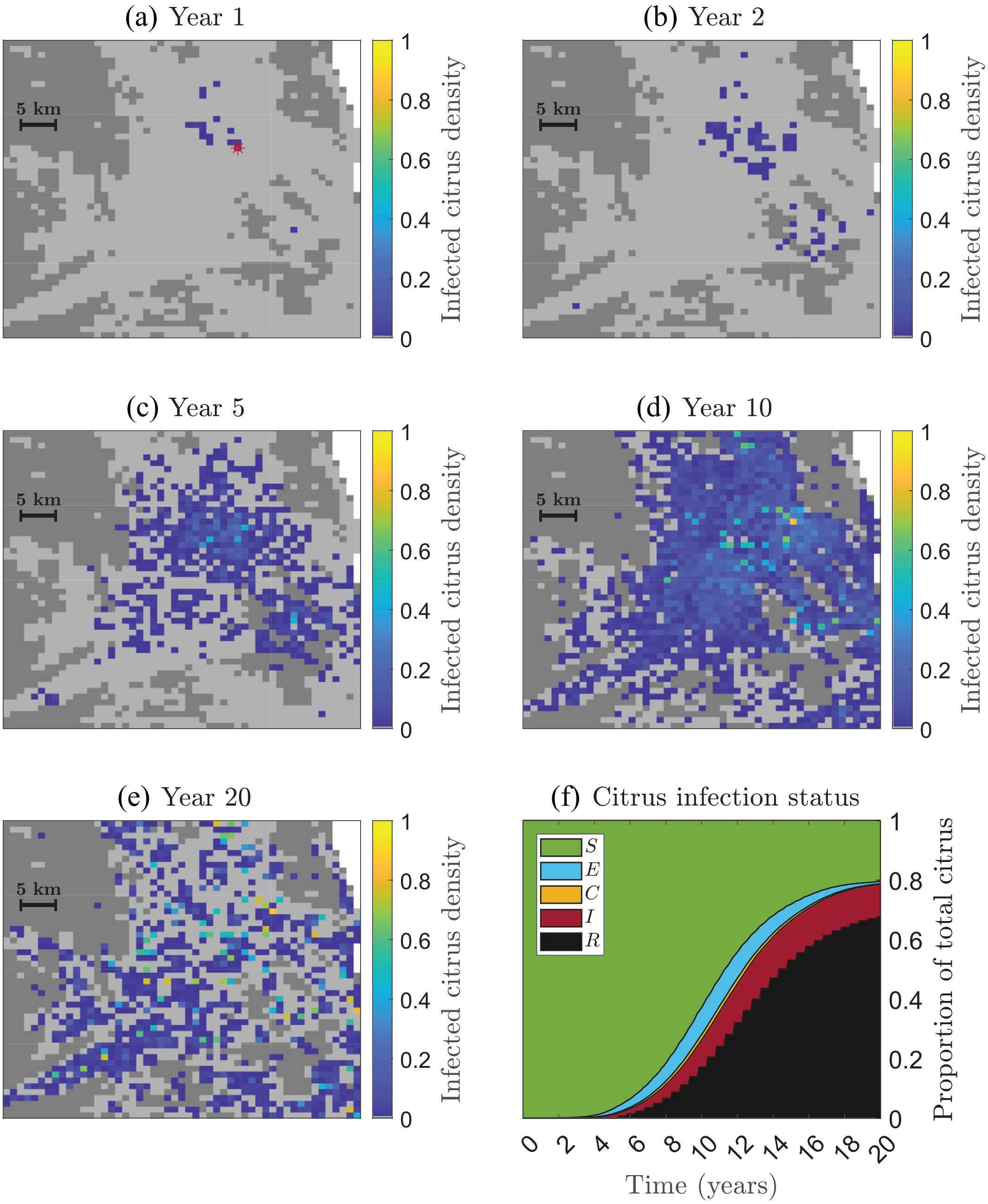

FIGURE 6 Spread of disease in a single simulation in Region A (Valencia) using baseline parameters for detection and control (Table 3). Initial conditions as Figure 3. In this simulation, disease is first detected after approximately 5 years, after which control started immediately. (a–e) Maps showing the density of infected citrus host units ($E + C + I$) within each cell at different times after introduction; see also Supporting Information Movie S3. (f) Disease progress curve showing proportions of citrus over the entire region in each epidemiological compartment, (S)usceptible, (E) xposed, (C)ryptic, (I)nfected and (R)emoved (i.e., rogued).

management effectiveness of sprays that are initiated as soon as detection occurs (m^*). By reducing the time before the pathogen is detected and control via roguing and spraying is initiated, epidemics become smaller when either the proportion of cells inspected (Figures 9a,b) or the probability of detecting positive psyllids given infection (Figures 9d,e) are increased. If early detection on psyllids is coupled with significant additional insecticide sprays, corresponding to extra management effectiveness of 90%, very good outcomes can be achieved (Figures 9c,f; top area of both figures). Similar results are obtained when the analysis is repeated for Region B (Supporting Information Figure S10).

4 | DISCUSSION

HLB has not been reported in the EU, although invasion is possible, perhaps even probable (Wang, 2020). We demonstrate how mathematical modelling can contribute to developing epidemiological

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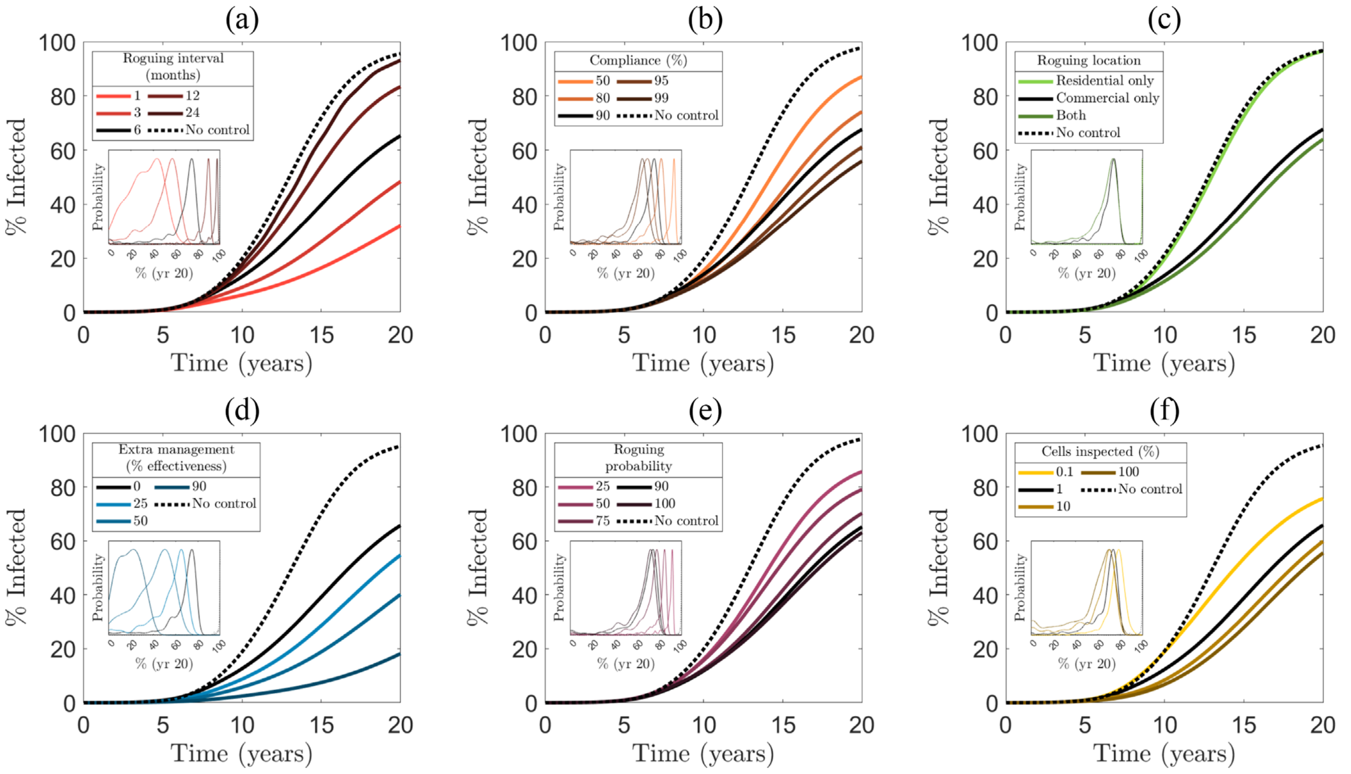

FIGURE 7 Management scenarios in Region A (Valencia). Mean proportions of infected or removed citrus ($E+C+I+R$, i.e., all host units that have ever been infected) over time when varying a single parameter from the baseline parameterisation (Figure 6 and Table 3). Aspects varied in each panel: (a) roguing interval, (b) grower compliance, (c) types of citrus rogued, (d) increases to the pest management parameter, m^*, (e) roguing probability and (f) proportion of cells inspected for early detection. Inset graphs show probability distributions of the proportion of infected or removed citrus after 20 years (normalised to have the same maximum for ease of visualisation). Black lines show results using the baseline parameterisation; dotted lines show results with no control. Averages and probability distributions calculated from ensembles 200 simulations per parameter combination.

preparedness for a future HLB invasion, focusing on regions in Spain containing high-density citrus production. We found that, at least in the absence of early detection via testing psyllids for CLas DNA, any epidemic is likely to be very well-established at the time of first detection. Even with intensive disease management with almost all commercial growers participating in a large-scale programme of detection and roguing (i.e., removal of infected citrus trees), eradication is very likely to be impossible. However, a combination of sustained and rapid disease control via roguing and very heavy insecticide sprays may provide relatively good control allowing sustained citrus production to be maintained for a decade or more, albeit with reduced production. This echoes the experience of growers and regulators at least some other countries, most notably Brazil (Bassanezi et al., 2020). Strategies accelerating early detection by testing psyllids for CLas DNA can be particularly successful, although heavy insecticide sprays would again be required to sustain production over long periods, and optimal results are obtained when this is combined by intensive roguing to remove sources of inoculum.

In the EU context, significant uncertainty surrounds the invading vector and bacterium. Although our model is transferable to different vector-bacterium combinations, we focused on invasion by CLas vectored by AfCP. Of the three CL species, CLas is the most widely distributed and damaging (Gottwald, 2010). Our choice should therefore be uncontentious. For the vector, we focused on AfCP, motivated by its presence in Portugal and Spain and despite recent reports of ACP from Israel (EPPO (European and Mediterranean Plant Protection Organization), 2022) and Cyprus (EPPO (European and Mediterranean Plant Protection Organization), 2023). Focusing on AfCP allowed us to use data from Spain and Portugal to parameterise long-range psyllid dispersal in our model. Although both vectors transmit CLas (Reynaud et al., 2022), the CLas-AfCP pathosystem is comparatively understudied and so systematic differences in CLas infection rates for AfCP *versus* ACP are not well-characterised. However, since our model explicitly includes vector climate suitability (Figure 1a), we account for AfCP's relative lack of heat tolerance (Paiva et al., 2020). Nevertheless, by focusing on the spatial variation in the proportion of AfCP "suitable" days over a long period, our model does not capture, for example, the possible local eradication of unestablished vector populations under sustained periods of high temperatures. Our model might therefore not fully capture AfCP population densities, despite being used previously in the region of interest (Galvañ et al., 2023). We used parameters and outputs from models of CLas vectored by ACP (Mastin et al., 2020; Nguyen et al., 2023) to parameterise short-range AfCP dispersal and

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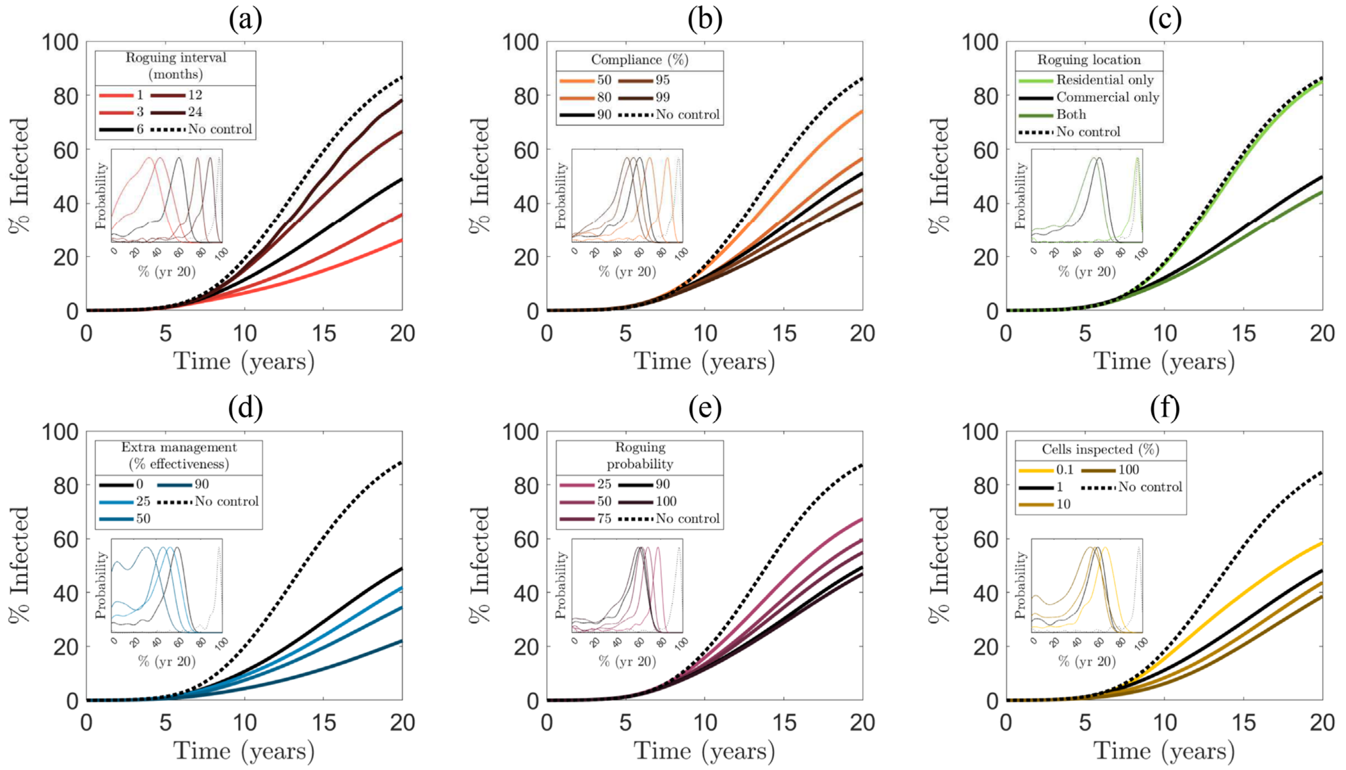

FIGURE 8 Management scenarios in Region B (Andalusia). Mean proportions of infected or removed citrus ($E+C+I+R$, i.e., all host units that have ever been infected) over time when varying a single parameter from the baseline case (Table 3). Individual panels as in Figure 7.

HLB transmission rates. While this was unavoidable, given the paucity of other information, it potentially understates biological differences between vectors. Although primary effects of climate on transmission will be via vector densities, we also do not explicitly consider any effect of temperature on CLas dynamics/bacterial titre within individual plants (Raiol-Junior et al., 2021). This might, of course, affect the dynamics, although we note that HLB is currently of significant concern in parts of California in the United States with rather similar climatic conditions to regions of Spain considered here (McRoberts et al., 2019).

Uncertainty also surrounds where HLB will first enter the EU. Although risks of entry have been modelled for the United States (Gottwald et al., 2019), there are no equivalent models for the EU, although nonpathogen-specific models are just starting to appear (Rosace et al., 2025). We therefore chose to focus on a reasonable worst-case scenario, with HLB introduced into high-density commercial citrus in Spain, the largest EU producer (Schimmenti et al., 2013). We compared results for two 50km × 50km regions, in Valencia and Andalusia (Figure 1), and (generally) assumed AfCP was already locally widespread at the time of HLB invasion. Our approach was intended to put limits on the potential efficacy of control. If the vector were also actively spreading in whichever area HLB was invading, as is arguably more likely, any outbreak would proceed slightly more slowly (Figure 4). However, as already noted, the relative efficacies of different management strategies are unaffected by prior invasion of the vector (Supporting Information Figure S4).

In fact, while AfCP has spread widely along the Atlantic coast of the Iberian Peninsula in the decade since detection (Benhadi-Marín et al., 2022; Perez-Otero et al., 2015; Siverio et al., 2017), it has not reached the main commercial citrus areas. Furthermore, (classical) biological control via the parasitoid *Tamarixia dryi*, as well as perhaps climatic effects, has slowed or even stopped spread in residential settings since 2019 (Duarte et al., 2024; Molina et al., 2021), although how *T. dryi* would be affected by insecticide sprays in commercial citrus is an important and understudied consideration. Simultaneous invasion of vector and pathogen has been common previously. For example, in California, ACP was first reported in 2008 and HLB in 2012 (Nguyen et al., 2023), while in Florida, ACP was reported in 1998 and HLB in 2005. However, the pathogen is harder to detect than the psyllid, and there is consensus that HLB was widespread in Florida by 2005 (Halbert et al., 2010).

The disease spreads rapidly in our model following first introduction (Figure 3). We note a recent expert knowledge elicitation exercise (EFSA (European Food Safety Authority) et al., 2019), which estimated a median spread rate of 20.61 km year^{-1} (1%–99% range 0.90–40.12 km year $^{-1}$) for HLB in the EU. While our spread rates are within this range, they lie towards the lower end, particularly early in invasions. There is a lag phase of a few years in which spread is relatively slow (Figure 4), particularly when the pathogen is introduced into cells with low citrus density. Of course, too, we might also note that sustained spread at 20km year^{-1} would be impossible to discern at the scale we have focused on here. By restricting our attention to

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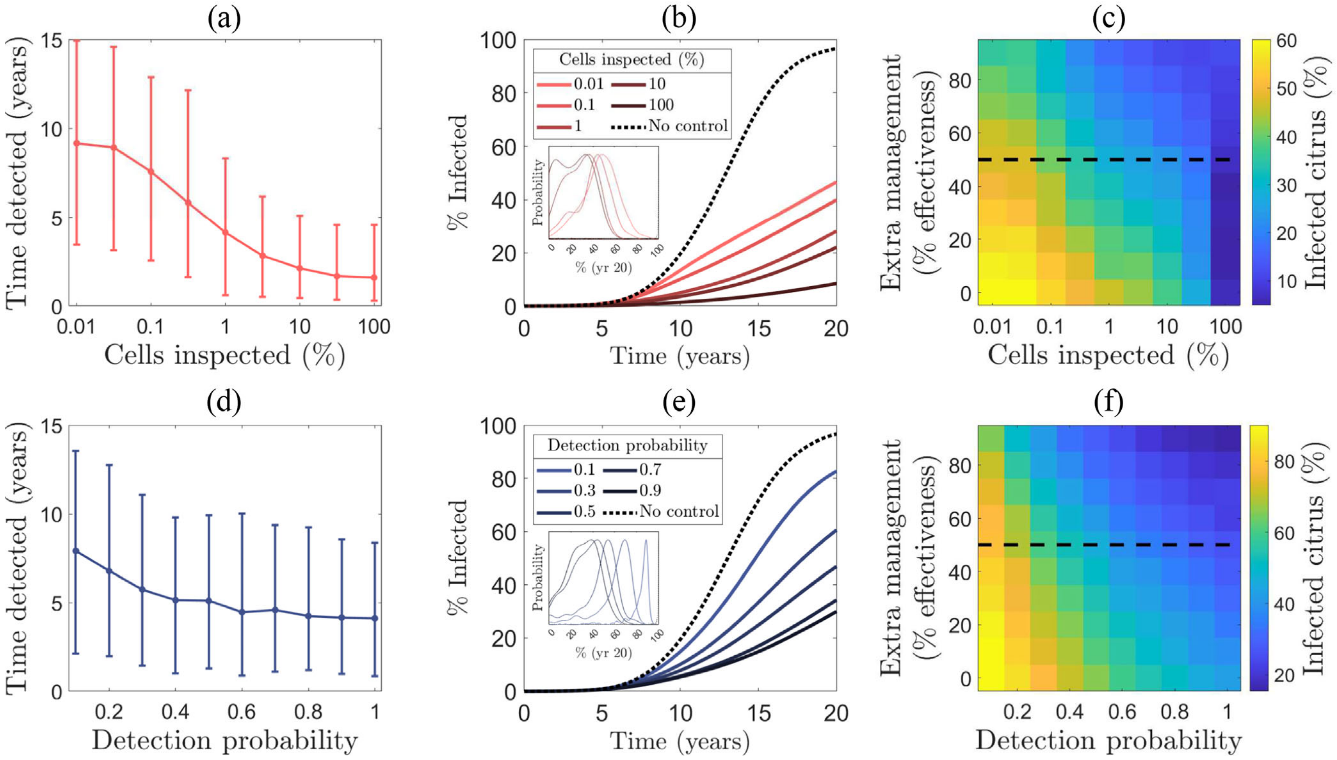

FIGURE 9 Testing vectors for *C*Las DNA as an early-warning system in Region A (Valencia). Mean time of detection and 95% prediction interval (Panels a and d) and proportions of infected or removed citrus ($E+C+I+R$, i.e., all host units that have ever been infected) over time (Panels b, c, e and f) when early detection is achieved by testing psyllids for *C*Las DNA and followed by additional insecticide sprays to reduce vector densities (as well as the other aspects of the baseline control strategy, e.g., six-monthly roguing). In (b) and (e), the extra management effectiveness (m^*) is 50% and plots correspond to parameters on the dotted lines in (c) and (f). In (a)–(c) the detection probability (p_v) is 0.9; in (d)–(f), 1% of all cells with citrus are inspected. Other parameters are as in the baseline parameterisation (Figure 6 and Table 3).

50km × 50km regions, we have tended to de-emphasise effects of long-distance dispersal, even though this is included in our model, and at larger scales, this would permit the disease to spread even more rapidly than 40 km year^{-1}. Given rates of long-distance psyllid spread in our model were calibrated to be sufficient to replicate the invasion over hundreds of kilometres of the Atlantic coast of the Iberian Peninsula within only 6 years, it is important to note that impacts of HLB invasion would rapidly be realised far outside the 50km × 50km regions of initial invasion we focused on here.

The delay before first detection of HLB depends on surveillance intensity but is 3–10 years for all parameterisations tested (Figure 5). The range is similar to, but the average again slightly lower than, estimates reported following the expert knowledge elicitation exercise (EFSA (European Food Safety Authority) et al., 2019), that is, a median of 2.1 years (1%–99% range 0.6–6.7 years). The lower bound of 3 years for detection in our model largely reflects the short lag before rapid spread in our model, as discussed above. We assumed that relatively large proportions of citrus were regularly being surveyed, and scaling this from our 50km × 50km regions to entire countries would be expensive. However, given we had no risk of entry based reason other than high-density commercial citrus to focus on the particular regions considered here, detecting the pathogen within these timescales would require an equally intensive country-wide survey, at least in regions of high citrus density. Since all three *C*Ls are EU Priority Pests, annual surveys are required in every Member State in which *Citrus* spp. are present (EU (European Union), 2016, 2019). However, currently recommended sample sizes are much smaller than those used in our study (MAPA (Ministerio de Agricultura, Pesca y Alimentaciòn), 2024). In contrast, we note that significant surveillance is currently mandated in the United States and Brazil (Bassanezi et al., 2020; Parnell et al., 2014) and given our results, we contend that surveillance in advance of invasion in the EU should be as intensive as reasonably possible (perhaps also including sampling vector populations for *C*Las DNA; see also below). In our model, cells are chosen for inspection at random, weighted by citrus density. However, other strategies, such as targeting locations at higher risk, may detect the disease earlier or with less cost (Mastin et al., 2020; Parnell et al., 2014). Testing this would be most informative if done over larger spatial scales, driven by a model quantifying relative entry risks (Douma et al., 2016).

In our default parameterisation, we modelled an immediate shift of strategy following detection, increasing surveillance and introducing disease control region-wide. The entire 50km × 50km region was therefore treated as the Infested Zone under Regulation (EU) 2016/2031 (EU (European Union), 2016). This is a simplification of current plans, which are based on bounding the infected area via a

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delimiting survey. Implementation of such surveys has become increasingly statistical (EFSA (European Food Safety Authority) et al., 2020) and is now based on identifying sample sizes required for a certain confidence in detection given an assumed disease prevalence. Recent work has tested performance of strategies for *Xylella fastidiosa* using a (small-scale) individual based model (Cendoya et al., 2024). Doing this for HLB would be interesting, and suitable small-scale models are already available (e.g., Craig et al., 2018; Parry et al., 2014), although recalibration would be needed for use in the EU.

Roguing does not stop the epidemic but slows spread (Figure 6). One driver is asymptomatic infection, since hosts are only detected and removed once symptoms are detectable. Another is that we assume that growers do not always comply with roguing infected trees, since HLB infected trees continue to produce fruit, at least for a few years (Bassanezi et al., 2011). Furthermore, private gardens, backyard trees and abandoned orchards act as refugia (Cocuzza et al., 2017). During an outbreak, there will be several locations where management does not occur, and these fuel spread. Nevertheless, even with perfect compliance by commercial growers and active management of residential citrus, transmission is likely to continue (Figures 7 and 8). This is due to the cryptic period within which plants are infectious but not symptomatic and so not detected/removed. Based on previous model fitting (Parry et al., 2014), we used a relatively lengthy asymptomatic period (1.25 years on average; Table 2). Detecting HLB before visual symptoms would improve performance (see also discussion of potentially accelerating detection by testing vectors for *C*Las DNA, below), even if diagnostic tests were inefficient (Mastin et al., 2022). Impressive results have been reported from Florida using dogs trained to identify infections before symptoms are visible (Gottwald et al., 2020). However, transferability and application over large spatial scales remain to be tested.

Asymptomatic infection means host removal could also be improved by removal of all trees within a particular radius of detected infection (Cunniffe et al., 2015). This is implicitly accounted for via our host quantisation, since roguing removes entire commercial host units (i.e., areas of $100\,\mathrm{m} \times 100\,\mathrm{m} = 1$ ha). However, modelling different radii of removal is relatively simple (Cunniffe et al., 2016; Hyatt-Twynam et al., 2017) and would be an interesting extension, perhaps particularly if coupled to more detailed models of grower behaviour (Murray-Watson et al., 2023) driven by information on factors affecting stakeholder opinions (Exilien et al., 2024; Garcia-Figuera et al., 2021). Current HLB contingency plans in Portugal and Spain (DGAV (Direção-Geral da Alimentação e Veterinária), 2021; BOE (Boletín Oficial del Estado), 2023) include a buffer zone surrounding the infested area within which intensive surveys and coordinated insecticide sprays should be applied. Modelling could again be used to optimise the size of the buffer zone and the type of surveillance to be applied within it and to provide quantitative support for contingency plans.

Slowing transmission by heavily controlling vector populations with additional insecticide is effective in our model (Figures 7d and 8d), as it has been (particularly) in Brazilian citriculture (Bassanezi et al., 2020). However, our model's representation of vectors might overstate efficacy. We do not model time-dependence in vector population dynamics, and so in turn, we assume that psyllid densities are immediately/simultaneously reduced in managed regions, ignoring difficulties of attaining such area-wide control (Galvañ et al., 2023) and of sustaining it over long periods. We also assume that psyllid populations can be reduced by up to 99%, without considering the frequency of sprays required, nor the expense, nor risks of insecticide resistance (which is now emerging in Brazil), nor the types of insecticide required to do so. Requisite chemical doses to achieve such reductions seem unlikely to be consistent with EU policies (Lázaro et al., 2021; Schneider et al., 2023). While Regulation (EU) 1107/2009 does permit emergency authorisation when a pest cannot be controlled by other means (EU (European Union), 2019), this applies for only a limited time and would likely be inconsistent with the sustained application over many years we consider here. Indeed, active ingredients currently labelled for citrus pests in the EU are less effective than those referred to for model parameterisation; most chemicals in Qureshi et al. (2014) are no longer marketed. Particularly noteworthy is the relatively recent EU withdrawal of the highly effective but also very environmentally damaging neonicotinoids (Butler, 2018); these chemicals have tended to have been required elsewhere for the highest levels of psyllid control (Miranda et al., 2016). In practice, it is also particularly difficult to protect flush (i.e., young and actively growing) leaf tissue favoured by psyllids and implicated in transmission (Cifuentes-Arenas et al., 2018), since the most commercially attractive (i.e., cheapest) insecticides are not systemic and do not cover rapidly growing tissue. However, controlling flushing frequency via selective pruning might provide partial mitigation (Matias et al., 2023). Given all this, it seems very likely that the highest levels of vector control considered here cannot be achieved with the chemical and biological tools currently available for citrus in the EU.

Targeting vectors for pathogen detection can be very effective in a range of epidemiological scenarios (Mastin et al., 2017). For HLB in particular, detection of psyllids carrying *C*Las DNA as an early-warning system of infection has been adopted in some areas of the United States (McRoberts et al., 2019). If a bacterialiferous psyllid infects a citrus plant and goes on to reproduce on the same plant, its offspring will feed on the flush leaves that have just become *C*Las infected. These offspring can therefore potentially acquire the bacterium even though only a very small part of the tree is infected (Lee et al., 2015). Lags between the initial HLB infection in a particular location and the local appearance of detectable numbers of *C*Las DNA positive psyllids can sometimes be measured in weeks (da Graça et al., 2015). This mechanism underlies the observation that detection of *C*Las DNA positive psyllids sometimes precedes detectable visible symptoms by months or even years (Keremane et al., 2015; Manjunath et al., 2008). Particularly when combined with additional insecticide spraying, our results suggest that accelerating detection of a first incursion via testing psyllids for *C*Las DNA can be very effective. However, a combination of knowledge gaps and the underlying structure of our model led us to use a highly phenomenological representation, in which we assumed that *C*Las DNA can detected over all psyllids trapped with a certain probability as

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soon as any infection is present in a cell from which vectors are sampled. Modelling this in more detail to allow for a more refined model of the probability of detection, for example, by including more detail on vector population dynamics and behaviour, as well as trap densities and number of psyllids captured, would be interesting. However, on the basis of the results presented here and elsewhere (EFSA (European Food Safety Authority) et al., 2024), the early-detection possibilities provided by vector sampling are clearly important and so should be factored into designing large-scale early detection strategies in the EU.

Despite many unavoidable uncertainties and some significant assumptions concerning disease spread and parameters controlling detection and control, modelling provides the only mechanism to understand how HLB might spread in the EU and to answer questions surrounding the best approach to detect and control any outbreak. We conclude that the most efficient management strategy would include early detection and intensive roguing to remove inoculum, alongside other measures to slow spread, particularly enhanced pest management to control psyllids. Especially good results can be obtained by accelerating first detection by testing vectors for *C*Las DNA, particularly if this is combined with widespread and effective insecticide sprays (albeit perhaps at levels of vector control inconsistent with EU regulations Lázaro et al., 2021). However, even this perhaps implausibly large degree of disease management seems very unlikely to eradicate any epidemic and confirms that ensuring engagement from growers is essential. Following first detection, and assuming as seems very likely that eradication proves not to be possible, the focus will shift to containment in order to sustain the citrus industry for the longest possible time in the face of HLB (Bassanezi et al., 2020). This is of course another area in which modelling can play a prominent role.

AUTHOR CONTRIBUTIONS

John Ellis and **Nik J. Cunniffe** designed the modelling framework and parameter estimation approach. **John Ellis** and **Nik J. Cunniffe** selected scenarios to test using the fitted model with input from **Elena Lazaro**, **Antonio Vicent** and **Stephen Parnell**. **John Ellis** developed and tested the computational code and performed all numerical simulations. **Elena Lazaro**, **Beatriz Duarte**, **Tomás Magalhães**, **Amílcar Duarte**, **Jactinto Benhadi-Marín** and **José Alberto Pereira** provided or processed citrus host and/or psyllid data. **John Ellis** and **Nik J. Cunniffe** wrote the manuscript, with input from all co-authors.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Code and data are available on GitHub https://github.com/DrJREllis/HLBinEurope.

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