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Accounting for spatially heterogeneous conditions in local-scale surveillance strategies: case study of the biosecurity insect pest, grape phylloxera (*Daktulosphaira vitifoliae* (Fitch))

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Abstract

BACKGROUND: Surveillance strategies are often standardized and completed on grid patterns to detect pest incursions quickly; however, it may be possible to improve surveillance through more targeted observation that accounts for landscape heterogeneity, dispersal and the habitat requirements of the invading organism. We simulated pest spread at a local scale, using grape phylloxera (*Daktulosphaira vitifoliae* (Fitch)) as a case study, and assessed the influence of incorporating spatial heterogeneity into surveillance compared with current, standard surveillance strategies.

RESULTS: Time to detection and spread within and beyond the vineyard were reduced by conducting surveys that target sampling effort in soil that is highly suitable for the invading pest in comparison with standard surveillance strategies. However, these outcomes were dependent on the virulence level of phylloxera because phylloxera is a complex pest with multiple genotypes that influence spread and detectability.

CONCLUSION: Targeting surveillance strategies based on local-scale spatial heterogeneity can decrease the time to detection without increasing the survey cost, and surveillance that targets highly suitable soil is the most efficient strategy for detecting new incursions. In addition, combining targeted surveillance strategies with buffer zones and hygiene procedures, and updating surveillance strategies as additional species information becomes available, will further decrease the risk of pest spread.

Supporting information may be found in the online version of this article.

Keywords: crop pests; invasive species; targeted surveillance; vector dispersal

1 INTRODUCTION

The ecological impacts and costs associated with biological invasions are expected to increase as trade and the human-assisted movement of invasive species continue to rise.[1] Therefore, it is essential to detect an incursion early, when its spread is limited and the likelihood of eradication or control is high, to decrease the potential of negative ecological, social and economic impacts.[2–4] To detect an incursion early, cost-effective and efficient surveillance is required. Surveillance designs or strategies are often based on collecting samples on either a grid or a random pattern. However, for regional-scale surveillance, more targeted strategies that account for spatial heterogeneity in land type (e.g. agriculture, forest, urban), species establishment rates or surveillance costs show increased ability to detect invasive plants[5] and reduce management costs.[6] It is possible that similar improvements to local-scale surveillance will be obtained through more targeted surveillance that accounts for heterogeneity within a field and focuses on the individual preferences and habitat suitability of the invading pest species.

We generally do not know where or when a new incursion is likely to occur next.[7] However, for many potential invasive species, we do know that only certain areas or locations in a landscape will provide suitable habitat or hosts. This is particularly relevant for

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biosecurity risk species that threaten specific crops. In these cases, it may be economically viable to conduct routine surveillance on suitable areas or locations, such as the properties where the host crop is grown or high-risk areas close to known infested regions, in order to increase the likelihood of detecting a pest when it is in low abundance.[8] In such cases, the benefits of targeted surveillance at the regional scale appear clear, but the possibility of further improving surveillance by also targeting the local scale has been limitedly explored.[9,10]

Grape phylloxera (*Daktulosphaira vitifoliae* (Fitch); hereafter referred to as 'phylloxera') is an invasive biosecurity pest that negatively affects the grape and wine industries worldwide.[11,12] Leaf (gallicole) and root-galling (radicicole) forms of phylloxera exist with root-galling phylloxera having an increased economic impact compared with leaf-galling forms because the radicicole feeds on the roots of susceptible vines disrupting nutrient and water uptake and causing extensive root damage. The only management option once an incursion is detected is to replant on resistant rootstock. Research on root-galling phylloxera has shown that population density varies with soil physical and chemical characteristics within a field (block), which suggests that targeted surveillance for high-risk areas at this scale may be effective.[9,10,13] Phylloxera is an ideal case study for investigating targeted surveillance because it spreads slowly without human-assisted or environmental vectors, its winged form cannot establish new infestations (thereby limiting the distance of spread), it feeds on a single host genera *Vitis* spp. (Vitaceae), its host is perennial and is in fixed locations (i.e. grapevine locations do not generally change between years), and phylloxera populations are patchy within a block due to variability in habitat suitability at a local scale.[12,14]

Furthermore, since the mid-19th century, phylloxera has spread from the eastern USA to grape-growing regions throughout the world, including Europe, Asia, Australasia, Africa and South America,[11,12,15] resulting in significant socio-economic impacts.[16,17] To decrease the negative impacts of phylloxera, most European grapevine *V. vinifera* cultivars planted worldwide are grafted onto phylloxera-resistant rootstocks derived from hybrids of American *Vitis* spp.[11] However, most rootstocks are not fully resistant to all phylloxera genotypes, and are regarded as tolerant (because they can still allow phylloxera colonies to reproduce and proliferate), and ungrafted *V. vinifera*, which is highly susceptible to phylloxera, is still widely planted in some grape-growing countries (e.g. ~85% of vines in Australia and China are *V. vinifera*; Powell KS, personal observation).[14] Therefore, phylloxera incursions continue to occur (Ararat Valley, Armenia, 2009[15]; Hunan, Shaanxi and Liaoning provinces, China, 2006–2007;[18] and the Yarra Valley, Australia, 2006–2017[12]; Powell KS, personal observation) even in regions where strict quarantine and hygiene regulations to prevent the movement of phylloxera vectors and contain the pest are present.[19] Current surveillance strategies generally only detect phylloxera when symptom expression is high and, hence, populations are abundant and have likely already spread to other blocks or vineyards where symptom expression may be relatively low.[20] Once an incursion occurs, eradication is almost impossible because phylloxera can persist within the soil profile even on excised roots from the surface to several metres down, has multiple generations and life-stages in a single year, and is relatively resistant to most chemical insecticides.[21] In the event of a phylloxera incursion, market access can be restricted (especially the movement of whole wine grapes, planting material and viticulture machinery)[19] and the cost of replanting onto grafted resistant rootstocks is relatively high.[15] Early detection of new phylloxera incursions is thus necessary to reduce further spread and maintain area freedom in regions that do not contain phylloxera, and reduce the costs associated with post-incursion phylloxera management. This is particularly essential in Australia where the distribution of phylloxera is currently limited to ~2% of all grape-growing regions (i.e. present in only some regions of Victoria and New South Wales).[19]

The spread of phylloxera is influenced by the virulence of the phylloxera genotype, the parentage of the host plant, the presence or absence of rootstock grapevines and environmental conditions,[14,22] particularly soil properties and temperature.[9,23–26] Phylloxera has multiple genotypes (83 in Australia)[27,28] that have different virulence levels, therefore representing a range of biological variants.[29] Under ideal conditions, less-virulent genotypes generally proliferate and spread slowly, and cause visual symptoms on vines much later than highly virulent genotypes. In addition, the spread of phylloxera may be slower if resistant rootstocks are present, high temperatures persist, and there is low electrical conductivity and potentially high soil pH.[9,24] The current surveillance strategy to detect phylloxera uses a specific fixed-density grid pattern and most research on phylloxera has been conducted in vineyards containing susceptible ungrafted *V. vinifera* and highly virulent phylloxera genotypes in ideal, cool climates (see Powell *et al.*[24] and Trethowan and Powell[30] for notable exceptions).[13,31] The possibility of improving local-scale phylloxera surveillance by targeting suitable habitat within the block still needs to be investigated, as do the effects of sampling density, phylloxera genotype virulence, vine susceptibility and temperature conditions on surveillance outcomes.

Field studies are time- and cost-intensive and can therefore only be applied to a very small sample of all fields and years. This makes it very difficult to design a field study that can clearly distinguish differences in outcomes between surveillance strategies over the wide range of possible conditions and incursion trajectories. Therefore, simulation modelling provides an essential tool for evaluating different surveillance strategies. Simulation modelling can be used to assess a wide range of scenarios that may include different patterns and/or levels of habitat suitability, ungrafted or grafted vines, more or less suitable climate conditions, different phylloxera genotypes, and different amounts of spread via vectors. Furthermore, simulation modelling allows us to consider the performance of surveillance strategies over a wide number of replicate simulations with exactly the same conditions. This allows us to understand the way that surveillance outcomes vary depending on the specific incursion trajectory and pattern that unfolds, which in turn depends on small stochastic differences in population dynamics and dispersal.

The aims of this study were to construct a local-scale model that simulates radicicole phylloxera spread through vineyard blocks and accounts for the most important drivers of spread, including vineyard configuration, wind- and human-vectored dispersal, soil type, phylloxera genotype and vine susceptibility, and then use this model to:

1. Investigate whether accounting for spatial heterogeneity can improve surveillance efficiency by comparing the detection efficacy of standard grid-based surveillance strategies with that of targeted spatially heterogeneous surveillance strategies that vary sampling density with soil suitability.
2. Assess how detection efficacy of surveillance strategies fluctuates as overall sampling density is varied.

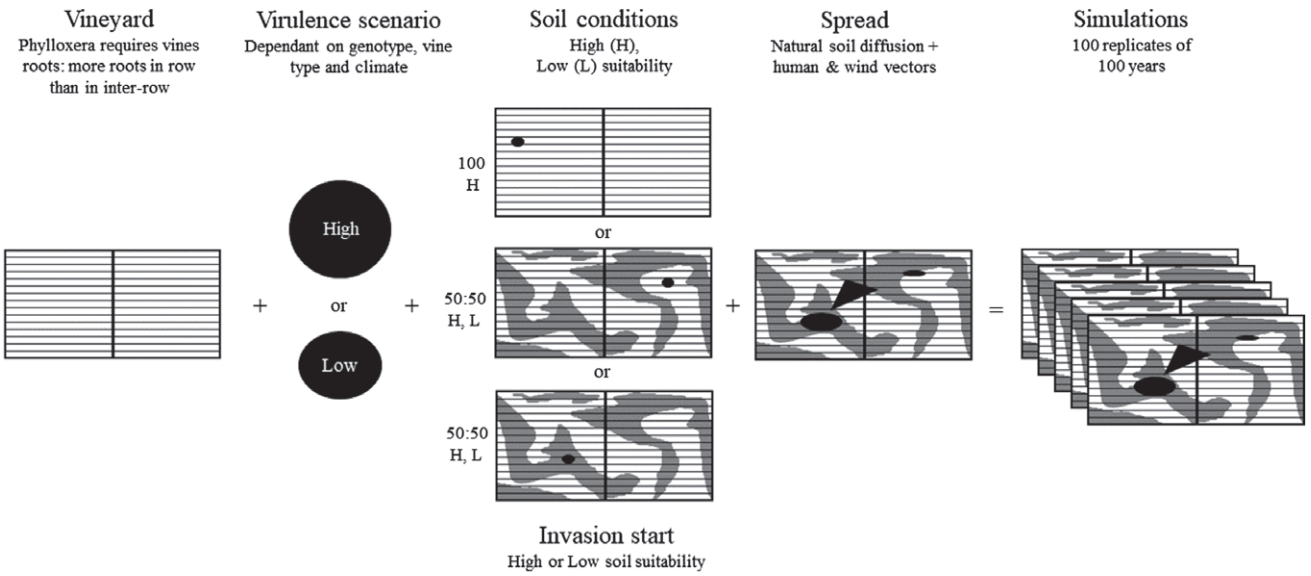

Figure 1. Schematic of the different simulations conducted in the study, including either high- or low-virulence root-galling phylloxera; either homogenous high-suitability soil (100:0 H, L) with initial location chosen at random or a heterogeneous mix of high- and low-suitability soil (50:50 H, L) with initial location chosen at random in either the high or low-suitability soil; vectors (only natural spread with human, via walking and machines, and wind spread was used in the end because this was the only dispersal scenario that produced realistic results) and 100 replicate simulations of each combination, each simulating spread over 100 years. In every case, the spread of phylloxera through two adjoining blocks of a vineyard from a single initial location is simulated. Note, this figure including vineyard rows is not to scale and is for illustrative purposes only.

3. Evaluate how the efficacy of surveillance strategies varies depending on soil suitability patterns and overall population growth rate as influenced by factors such as the virulence level of the phylloxera, vine susceptibility, climatic suitability, soil suitability and initial incursion location.

2 MATERIALS AND METHODS

2.1 Important characteristics of phylloxera spread

Typically, new radicicole phylloxera incursions result from the transfer of phylloxera to a location in a vineyard via human or environmental vectors.[20,32] If soil conditions at the initial site of an incursion are suitable, phylloxera reproduces and spreads as the first instar life-stage to the surrounding vines,[20,23] and if soil is less suitable, phylloxera will spread at a reduced rate. Generally, virulent phylloxera genotypes spread faster than the rate at which vines decline under their impact, and therefore, visual symptoms may underestimate the distribution of phylloxera.[11] As the invasion progresses, vine roots die in the epicentre, forcing phylloxera to expand outwards to locate food, resulting in radial spread and the highest density of phylloxera being pushed to the edges of the invasion.[11] The movement of phylloxera occurs on infested vines, through soil, contaminated soil on workers' clothing or machinery, infested soil via erosion and wind, with most long-distance movement occurring via humans and environmental vectors.[20] These vectors can move phylloxera-infested soil and foliage within one vineyard or to new vineyards. Environmental vectors such as the prevailing wind[11,23] and the direction of irrigation and water flow[23] also increase the potential for phylloxera movement in particular directions.[33] After phylloxera has infested a new area, its spread is dependent on interactions between the phylloxera genotypes,[34] vine type (rootstock or own roots), environmental conditions, such as temperature and soil properties, in the area,[35] and the movement via human and environmental vectors.

Table 1. Index of habitat suitability based on soil suitability and position within the vineyard

Soil suitability	Vine row	Inter-row
High suitability	1.00	0.20
Low suitability	0.10	0.02

2.2 General model structure – phylloxera spread

We developed a spatially explicit model in R[36] to simulate the potential spread of first instar phylloxera through a landscape with different soil suitability levels (Fig. 1). The model represents the landscape as a grid of square cells (1.3 m × 1.3 m), each of which is associated with a number of phylloxera that can change with time, and a habitat suitability index that depends on soil suitability and whether the cell is in the vine or inter-row (Table 1). The model simulates spread from one year to the next, although for implementation purposes time is subdivided into a number of time steps per year. At each time step, population growth is modelled separately within each grid cell, based on several model parameters: an estimated annual growth rate ($annual_{growth}$), the maximum possible population within a grid cell (max_{pop}) and the number of time steps ($time_{step}$). The rate at which the population increases at each time step ($rate_{increase}$) is estimated by:

$$rate_{increase} = annual_{growth}^{(1/time_{step})} - 1 \quad (1)$$

The natural spread of phylloxera through the soil is also modelled as diffusion between adjacent grid cells, based on two model parameters: the annual chance of diffusing ($annual_{diffuse}$) and the number of time steps in each year ($time_{step}$). The chance of a phylloxera moving to an adjacent cell via natural diffusion at each time step ($chance_{diffuse}$) is:

$$chance_{diffuse} = annual_{diffuse}/time_{step} \quad (2)$$

The maximum phylloxera population for each cell at a $time_{step}$ is estimated by multiplying max_{pop} by the cell's habitat suitability index (see Table 1). For each grid cell, the increase in individuals in that cell ($increase_{cell}$) is selected at random from a Poisson distribution, using the R function *rpois*, based on $rate_{increase}$, the habitat suitability index for the cell, and the current number of individuals in the cell (n_t):

$$increase_{pixel} = rpois\left(n_t \times rate_{increase} \times habitat\ suitability\right) \quad (3)$$

The new number of individuals in the cell is simply $n_t + increase_{cell}$. The value of max_{pop} is then subtracted from this new number to determine the number of 'extra' individuals that have an increased likelihood of moving to a different cell:

$$extras = \text{maximum}\left(0, \max_{pop} - \left(n_t + increase_{cell}\right)\right) \quad (4)$$

The number of 'normal' individuals moving from each grid cell is selected at random from a binomial distribution, via the R function *rbinom*, so that the total number of individuals moving from the cell via diffusion (i.e. not via vectors) at that time step is:

$$diffusers = rbinom\left(n_t + increase_{cell}, chance_{diffuse}\right) + extras \quad (5)$$

The number of diffusing phylloxera moving in each of the four possible directions (north, south, east or west) is then randomly selected from a multinomial distribution.

Phylloxera can be picked up and spread via human (walking or machinery) or environmental (wind) vectors. There are other potential vectors for human and environmental spread, but we identified these as the most likely source of spread at this scale. Spread via human vectors is modelled using two methods: (i) workers moving and potentially spreading phylloxera in a back and forth pattern along inter-rows; and (ii) machinery (e.g. harvester) moving and potentially spreading phylloxera in a spiral pattern, representing the machinery's need for a larger turning circle (see Fig. S1) between rows. The modelled human vectors have the potential to accidently pick up and carry phylloxera encountered at any point along their path, with a probability of $p_{humanpickup}$. This picked-up phylloxera is then carried along the path and has a chance to be dropped and to establish, with a constant probability $p_{humandrop}$ at any given point along the path. For each cell along the path, the numbers picked up $n_{humanpickup}$, dropped $n_{humandrop}$, and carried from that cell to the next $n_{humancarry}$ are thus calculated as:

$$n_{humanpickup} = rbinom\left(n_t + increase_{cell}, p_{humanpickup}\right) \quad (6)$$

$$n_{humandrop} = rbinom\left(n_{humancarry}, p_{humandrop}\right) \quad (7)$$

$$n_{humancarry} = n_{humancarry} - n_{humandrop} + n_{humanpickup} \quad (8)$$

The number of phylloxera spread by wind (n_{wind}) is calculated using a binomial distribution dependent on the likelihood of phylloxera being picked up by wind ($p_{windpickup}$). Each phylloxera that is picked up by wind is then deposited at a new cell at a distance and angle from the origin cell, which are drawn at random, and independently, from Cauchy and VonMises distributions, respectively:

$$n_{wind} = rbinom\left(n_t + increase_{cell}, p_{windpickup}\right) \quad (9)$$

Table 2. Model parameters and their values defined after parameterization of the model based on expert opinion

Parameter	Value	Explanation
$annual_{growth}$	8; 2	Increase in growth per year (high and low virulent, respectively)
max_{pop}	10 000	Maximum population per grid cell
$time_{step}$	4	Movement events per year
$annual_{diffuse}$	0.001	Likelihood of 'natural' diffusion to adjacent grid cells
$time_{years}$	100	Time span of the simulations
$p_{humancarry}$	0.0001	Probability of being picked up and carried by a human or machine
$p_{humandrop}$	0.00001	Probability of being dropped by a human or machine
p_{detect}	1.0, 0.75, 0.50, 0.25	Probability of detection – results for 0.75 shown
$p_{windpickup}$	0.00001	Probability of being picked up and carried by the wind
a	1	Cauchy scale parameter (wind strength)
d_{wind}	pi/4	Mean direction of the VonMises distribution (wind direction – southeast)
b	100	Concentration parameter of the VonMises distribution (wind direction consistency)

$$\text{distance} = abs\left(rcauchy\left(n = n_{wind}, 0, a\right)\right) \quad (10)$$

$$\text{angle} = as.numeric\left(rvonmises\left(n = n_{wind}, mu = circular\left(d_{wind}\right), \text{kappa} = b\right)\right) \quad (11)$$

where a, b, d_{wind} are fixed model parameters representing median dispersal distance, wind direction consistency and prevailing wind direction, respectively.

Through a series of discussions between the modellers and the biological experts on the project team (the authors), a set of model parameter values was developed. These values represent the rate and patterns of phylloxera spread to best match available data and past observations across a range of locations, with a prevailing wind from the southeast and a maximum dispersal distance of 30 m (Table 2).[33,37] This general parameterization was suited to the study's aim of making general recommendations, but all parameters, particularly for vector movement, could be specified to represent specific individual field/block conditions if required (see Fig. S2 for an example of the influence of individual dispersal type on spread distance in this model).

2.3 Phylloxera spread simulations

Using the calibrated model described above, we ran different phylloxera spread simulations. All simulations represented the growth and spread of a new phylloxera population in a hypothetical landscape, which represents a vineyard with two blocks of grapevines, each covering 1.74 ha. The blocks are separated by a 3.9 m strip and there is a 65 m buffer around the whole simulated area; these areas

Table 3. The nine surveillance strategies assessed. Variations of the standard strategy either increase or decrease sample density and targeted strategies denote surveillance that targets soil suitability. The 'proportion compared to standard' represents the increase or decrease in the number of samples required for each surveillance strategy compared with the standard. For example standard^{++} has 92 samples vs the standard which has 40 samples, this means it requires 2.3× the number of samples/effort/cost as the standard. Soil conditions including soil type, temperature, chemistry, texture and moisture influence the ability of phylloxera populations to establish and grow (Table S1). Therefore, the 'Soil suitability' column shows which soil-type scenario was considered, where '50:50' indicates a heterogeneous soil scenario with 50% high- and 50% low-suitability soil only and 'Both' indicates that the strategy was run for all soil type scenarios (50:50 and 100:0 high : low suitablility soils)

Surveillance	Samples/ha	Proportion compared to standard	Soil suitability	Details
Standard	40	Ref	Both	Third row fifth panel
Standard^{+}	61	1.53	Both	Second row fifth panel
Standard^{++}	92	2.30	Both	Second row third panel
Standard^{-}	30	0.75	Both	Fourth row fifth panel
Standard^{--}	23	0.58	Both	Fourth row seventh panel
Targeted 30/10	40	1	50:50	30 samples in high-suitability soil, 10 samples in low-suitability soil
Targeted 10/30	40	1	50:50	10 samples in high-suitability soil, 30 samples in low-suitability soil
Targeted 40/0	40	1	50:50	40 samples in high-suitability soil, 0 samples in low-suitability soil
Targeted 0/40	40	1	50:50	0 samples in high-suitability soil, 40 samples in low-suitability soil

do not contain grapevines and represent roads or bare ground that have no food source for phylloxera to persist. Each block is made up of 10 300 (103 rows × 100 columns) square grid cells (1.3 × 1.3 m). There are 51 vine rows in each block, and 52 inter-rows (i.e. the space in between the vine rows), each of which is represented by a single row of grid cells. We assume there is a single grapevine in the middle of each cell of the vine row, which results in a 2.6 m spacing between vine rows and 1.3 m between grapevines within the row. Inter-row cells are assumed to be less suitable for phylloxera because they contain fewer grapevine roots (Table 1). In reality, root density in the inter-row is likely to be influenced by irrigation, soil profile and the age of the vines, and the phylloxera habitat suitability in the inter-row could be adapted for specific vineyards depending on these variables.

Soil conditions, including soil type, temperature, chemistry, texture and moisture, influence the ability of phylloxera populations to establish and grow (Table S1). In the model, these factors were simplified by considering just high and low soil suitability (Table 1). We considered two landscapes with different soil properties: one homogeneous and one heterogeneous (100:0, 50:50 high : low suitability soil, respectively) (Fig. 1). As discussed previously, a range of environmental and genetic factors influences the rate of phylloxera growth and spread, but for modelling, we simplified this by considering just 'high-virulent' and 'low-virulent' phylloxera scenarios. The high-virulent scenario represents a virulent genotype that spreads relatively quickly, in ideal, cool climate conditions and on *V. vinifera* or a rootstock that does not restrict the spread of that particular genotype. A low-virulent scenario represents a less-virulent genotype that spreads relatively slowly, occurs in predominantly warm climate conditions on roots that restrict the spread of that particular phylloxera genotype. We explored four possible dispersal scenarios: natural soil diffusion only, natural soil diffusion plus human vectors, natural soil diffusion plus wind spread, and natural soil diffusion plus human vectors plus wind spread. Only the scenario with combined natural soil diffusion, wind and human vectors was realistic in its representation of phylloxera spread and so all analyses presented below used this dispersal scenario.

For every set of conditions, 100 replicates of phylloxera spread were simulated over 100 years (Fig. 1). For simulations with homogeneous soil, the initial location of the incursion was chosen at random in each of the 100 runs. For simulations with heterogeneous soil, preliminary analysis showed that whether the incursion started in the high- or low-suitability soil has a large influence on outcomes, and so 100 simulations were conducted with a starting location chosen at random within the high-suitability soil, and another 100 simulations with a starting location chosen at random within the low-suitability soil. The total number of simulations conducted was thus 2 virulence levels × 3 soil scenarios × 1 dispersal scenario × 100 replicates = 600 (Fig. 1).

2.4 Surveillance

The standard nationally endorsed phylloxera surveillance protocol is to sample the roots of a single vine within every fifth panel (one panel equals ∼ 5 m) of every third row, as well as any visibly weak vines.[17] In regions where phylloxera is known to occur (i.e. vineyards located near infested vineyards), surveillance is often completed annually, but surveillance may not occur at all in regions where phylloxera has not been detected previously. Therefore, new detections are highly dependent on vineyard location; additionally, surveillance frequency is determined by the vineyard manager. We considered a number of surveillance strategies, including the standard grid-based strategy and eight alternatives that either varied sampling density by increasing or decreasing the number of samples per row and/or panel, or accounted for spatial heterogeneity by targeting locations based on soil suitability (see Table 3 for descriptions). In the simulated study area, standard surveillance resulted in a density of 40 samples per ha, therefore all spatially heterogeneous (targeted) surveillance strategies also contained 40 samples per ha to enable direct comparison. All grape phylloxera spread models and surveillance codes can be accessed via the University of Western Australia's research repository.[38]

2.5 Phylloxera spread and surveillance

To compare surveillance strategies, each spread simulation for both homogeneous and heterogeneous soil and high- and low-virulent scenarios was combined with the nine surveillance strategies independently. We considered four different detection probabilities (perfect, 1.00; or imperfect, 0.75, 0.50 and 0.25) separately for each surveillance strategy. If detection probability was

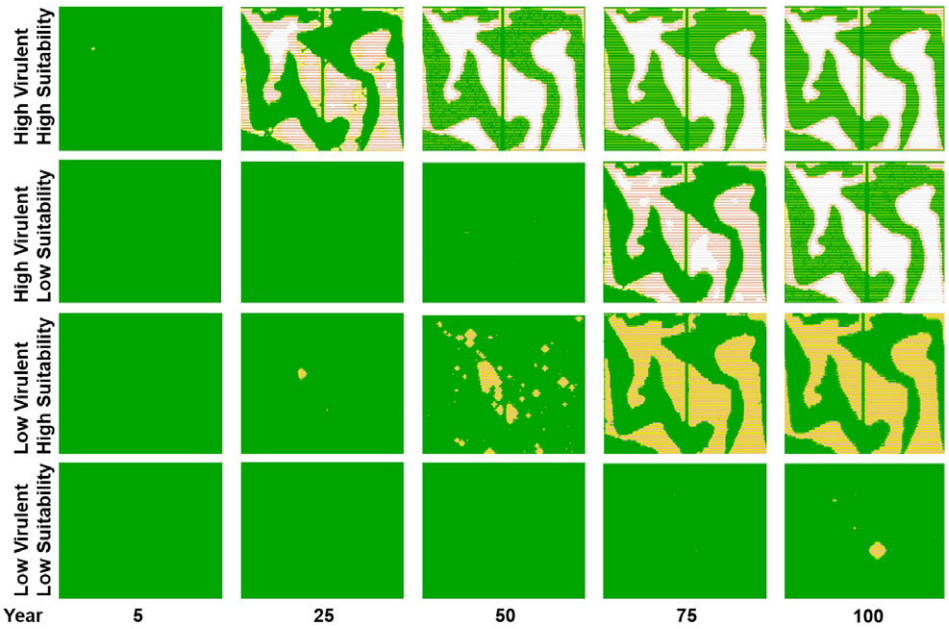

Figure 2. The spread of phylloxera over the simulated landscape with 50:50 high : low suitability soil under either a low- or high-virulent scenario. The indication of 'low' or 'high' suitability indicates in which soil type the incursion begins. Each green square represents alternating vine rows and inter-rows in a vineyard block. The initial phylloxera incursion starts in one cell and as the abundance of phylloxera increases, cells change colour from yellow (phylloxera abundance = 1–5000) to orange (phylloxera abundance = 5000–10 000) and finally white (phylloxera abundance >10 000), which indicates the phylloxera abundance is greater than the maximum population defined per time step. The spread of phylloxera is shown at 5, 25, 50, 75 and 100 years post incursion.

perfect, the first time that any cell was both under surveillance and infested was recorded as the time of first detection. If detection probability was imperfect, then whether detection actually occurred at a given time was determined stochastically for every cell that was both under surveillance and infested at that time. When the first detection occurred, we recorded:

1 Number of years from initial incursion to detection.
2 Maximum distance spread (m).
3 Total area infested (m^2).
4 Number of panels infested.
5 Number of rows infested.
6 Total cumulative number of phylloxera carried out of the simulated area by human vectors (i.e. the number picked up by humans or machinery but never dropped and thus still carried when they reached the end of their path through the vineyard blocks).
7 Total cumulative number of phylloxera carried beyond the simulation area by wind (i.e. the number carried beyond the vineyard blocks and the 65 m border).

In total, seven output values were recorded for 100 replicate runs of 216 different combinations (9 surveillance strategies × 4 detection probabilities × 2 virulence levels × 3 soil scenarios × 1 dispersal scenario).

If detection did not occur at all within 100 years, then the time was recorded as > 100, the number of phylloxera spread beyond the vineyard and the within-vineyard spread were recorded as the value at 100 years. Cumulative distributions of variables from each alternative strategy were then compared with the cumulative distribution for the standard strategy, using the Kolmogorov–Smirnov test (K–S test) to determine if the distribution of results differed significantly from those of the standard strategy with a detection probability of 0.75.

3 RESULTS

3.1 Spread simulations

In the 100:0 suitable soil scenarios, phylloxera incursions always began in suitable soil as all cells in this scenario are defined as high-suitability soil, and thus spread from their initial location at a rate that depends on the virulence of the scenario – quickly in the high-virulent scenario and more slowly in the low-virulent scenario. In addition to differences caused by virulence level, phylloxera spread in the 50:50 soil suitability scenario is influenced by the arrangement and availability of suitable soil and the location of the initial incursion, with much slower spread when the initial location is in the low-suitability soil (Fig. 2).

3.2 Targeted surveillance strategies

In high-virulent scenarios when the incursion began in high-suitability soil the incursion was detected by year 25; however, when the incursion began in low-suitability soil it was not always detected by year 100 (Fig. 3). A similar trend was determined in low-virulent scenarios and within these scenarios incursions that began in high-suitability soil were not detected after year 50 and the majority of incursions that began in low-suitability soil were not detected after 100 years (Fig. 3).

Overall, the results show that time to detection, spread within the vineyard (including maximum distance, total area, the number of rows and the number of panels) and spread beyond the vineyard could be reduced in comparison with the current non-targeted standard strategy by conducting surveys that focus sampling effort in high-suitability soils (Fig. 4). For example, incursions were detected earlier (Fig. 4a) and had spread less at the time of detection (Fig. 4b–e) with the targeted 40/0 strategy (all surveillance in high-suitability soil) compared with the standard strategy. Reduced time to detection compared with the standard strategy was observed in strategies that targeted high-suitability

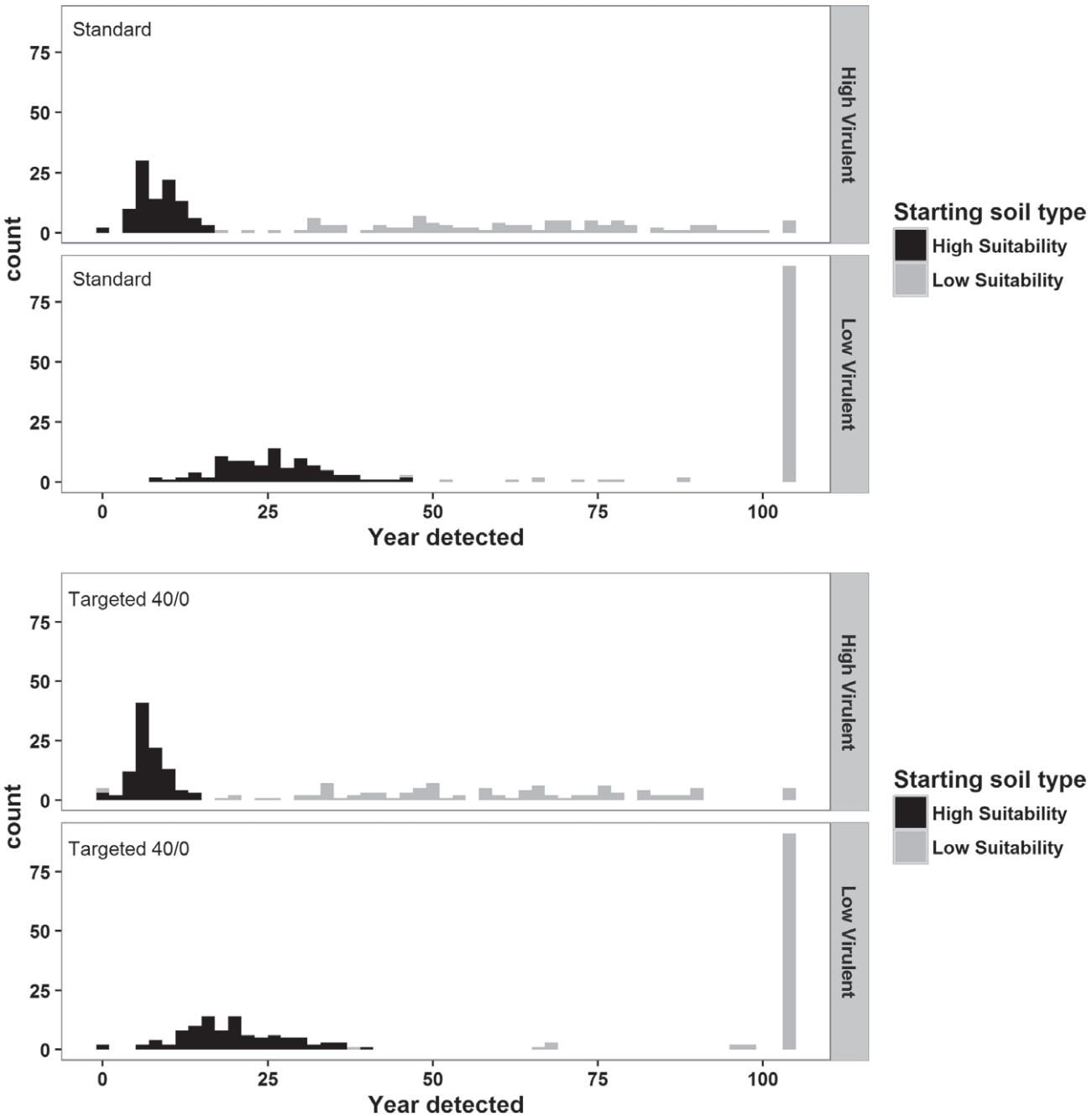

Figure 3. An example of the distribution of phylloxera detections obtained with the standard (upper) and targeted 40/0 (lower) surveillance strategies for high- and low-virulent scenarios in 50:50 high : low suitability soil. The location of the incursion start are represented by black (high suitability) and grey (low suitability) bins with a bin width of 2.

soil in simulations of both high-virulent (targeted 40/0, $P < 0.001$ and targeted 30/10, $P = 0.012$) and low-virulent scenarios (targeted 40/0, $P = 0.012$; Fig. 4a). Conversely, time to detection and area infested were no different or worse than for the standard strategy when using a strategy that focused sampling effort in low-suitability soils. Compared with the standard strategy, in strategies that targeted only low suitability, time to detection increased in both high-virulent (targeted 0/40, $P < 0.001$) and low-virulent scenarios (targeted 0/40. $P < 0.001$; Fig. 4). Strategies that targeted high-suitability soil also resulted in decreased numbers of phylloxera carried beyond the simulation area before the time of detection, and strategies that targeted low-suitability soil resulted in increased numbers of phylloxera carried beyond the simulation area, compared with the standard strategy (Fig. 5a). These trends were observed in both high- and low-virulent scenarios (Fig. 5a). More phylloxera were carried out of the vineyard by machinery than by humans or wind (wind only accounted for one or two instances of spread beyond the vineyard per simulation). The difference between humans and machines was because machinery travels down vine rows, whereas the humans walk down inter-rows that contain fewer phylloxera; however, this can be updated in the model to reflect the likelihood of vector movement. No phylloxera ever moved out of the vineyard by themselves because of their short-range diffusive movement.

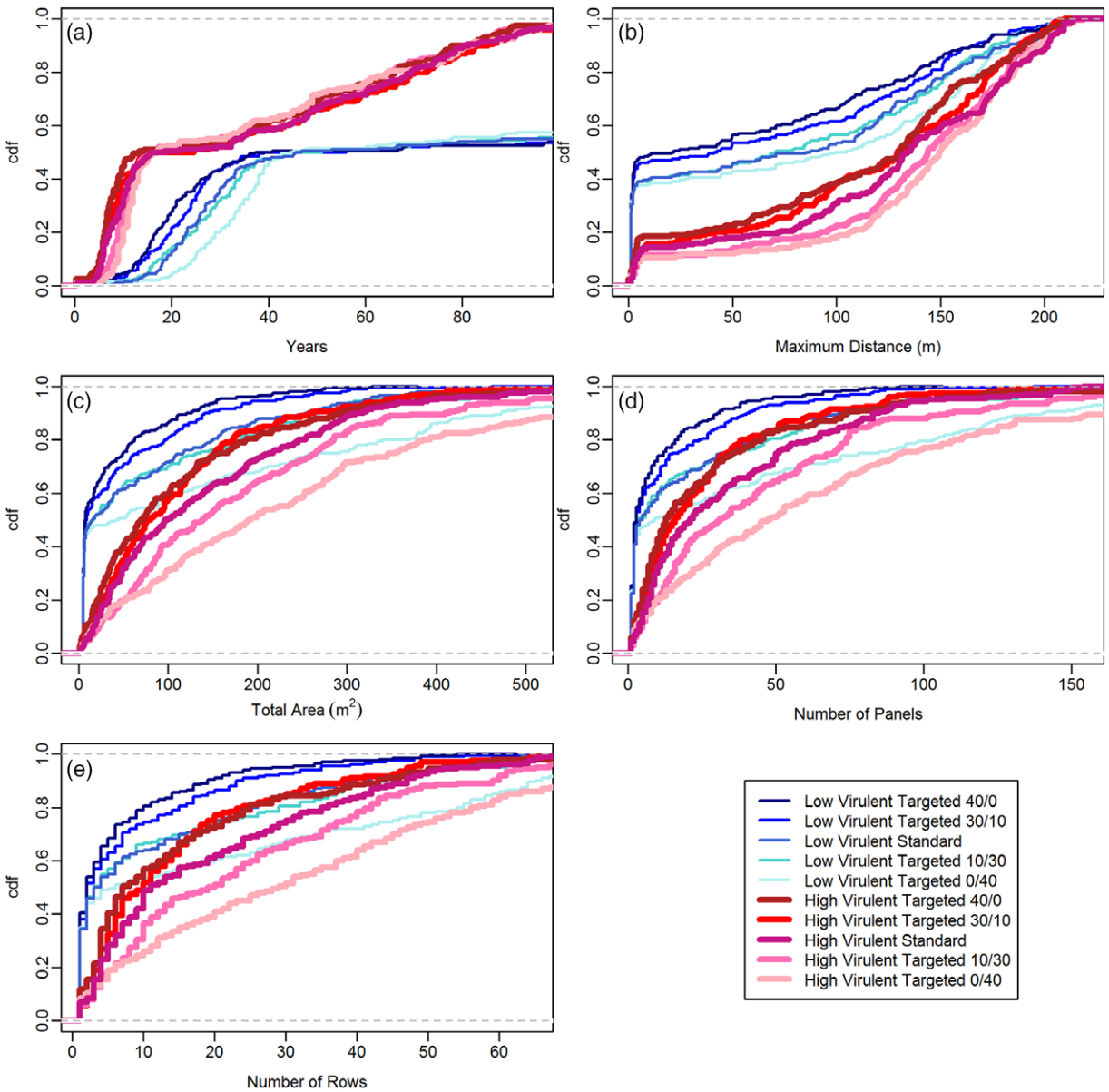

Figure 4. Results for all surveillance methods that target soil suitability and the current standard in a landscape with 50:50 high : low suitability soil and a 0.75 detection probability. The plots show the realized cumulative distribution function (cdf), with the *y*-axis indicating the cumulative probability. Initial detection time is represented by the number of years until the first detection occurs (a). Values for maximum distance travelled (b), total area infested (i.e. number of cells that were infested) (c), and the number of panels (d) and rows infested (e) were all calculated at the initial detection time. All strategies have 40 samples/ha and the location of these samples in high- or low-suitability soil is referenced in the legend as 'high : low'. Lines that are further to the left indicate better surveillance outcomes (smaller time or spread for a given probability).

3.3 Sampling density

In general, time to detection and spread within the vineyard decreased as sampling density increased, in both 50:50 (Fig. 6) and 100:0 (Fig. 7) suitability soils. Spread beyond the vineyard also decreased as sampling density increased, in both soils and both virulence scenarios (Fig. 5b,c). However, in the 50:50 suitability soil there was no significant difference between the standard^{++} and the much lower density targeted 40/0 strategies in simulations of either virulence level.

3.4 Virulence levels and starting location

Surveillance outcomes were highly influenced by phylloxera virulence level (Figs 2–7). For example, in a heterogeneous soil, incursion was detected ~ 45–55% of the time in low-virulent scenarios, but > 95% of the time in high-virulent scenarios (Figs 3, 4a, 6a and 7a). Detection occurred earlier in high-virulent scenarios compared with low-virulent scenarios, for all surveillance strategies, regardless of the percent of high- and low-suitability soil in the landscape (Figs 3, 4a, 6a and 7a). The relationship between virulence and the amount of spread within the vineyard at first detection (i.e. maximum distance spread, number of invaded rows, panels and area) was less consistent (Figs 4, 6 and 7). In heterogeneous soils, there was generally more spread at time of detection in high-virulent scenarios than in low-virulent scenarios, for any given surveillance strategy, with differences in maximum distance being most clear (Figs 4 and 6). By contrast, in homogeneous soils, there were no clear overall differences in spread outcomes

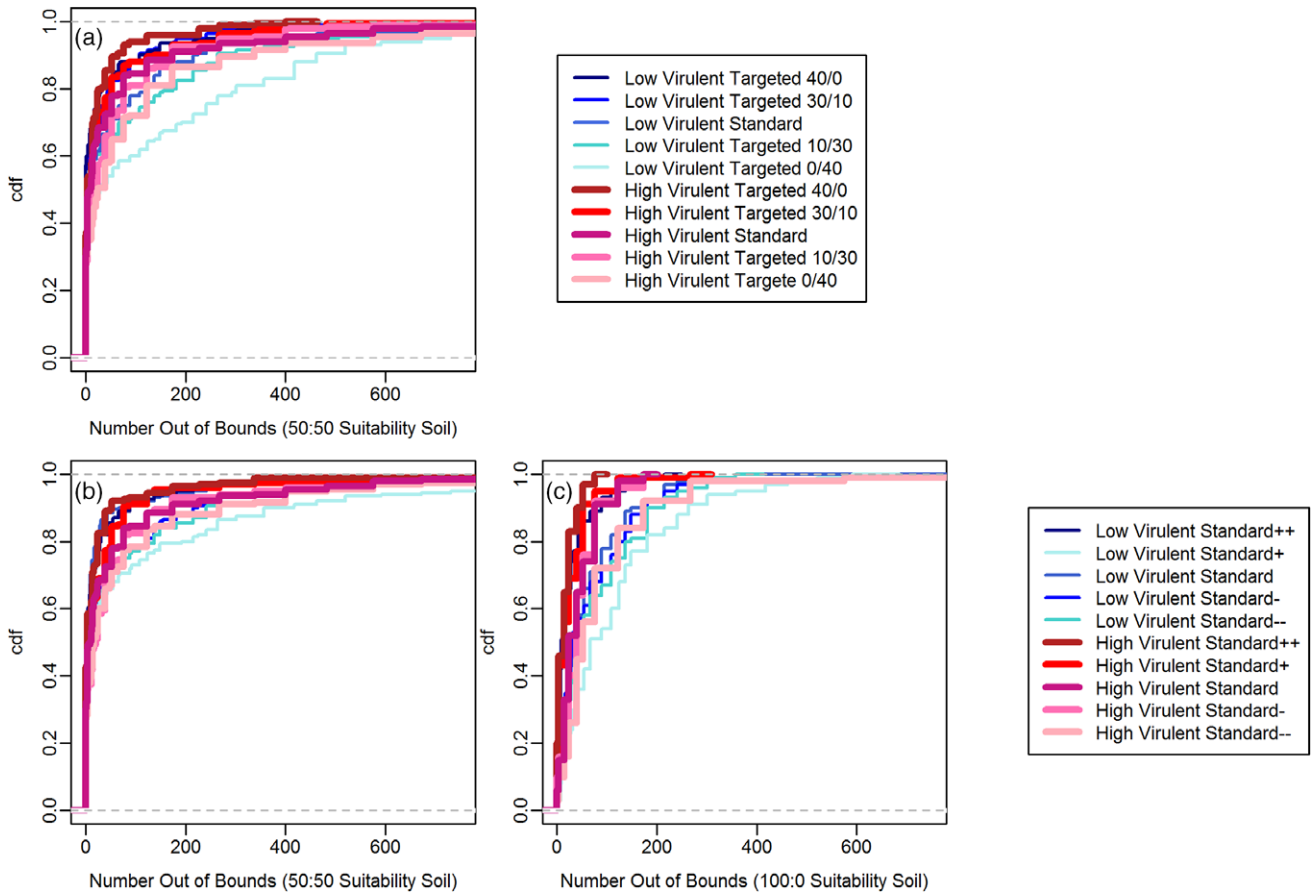

Figure 5. Number of phylloxera carried beyond the simulation area at the time of detection, for surveillance strategies that targeted soil types (a) and that varied sampling density (b,c). The plots show the realized cumulative distribution function (cdf), with the *y*-axis indicating the cumulative probability. Lines that are further to the left indicate better surveillance outcomes (smaller spread for a given probability).

between high- and low-virulent scenarios, but sampling density had a greater impact on spread outcomes (differences between higher and lower sampling densities are larger) in high-virulent scenarios than in low-virulent scenarios (Fig. 7b–e). Increased virulence seemed to decrease spread resulting from high-density sampling, but possibly increase spread resulting from low-density sampling; this is likely related to the time of detection because high-density sampling resulted in an earlier time of detection, on average. Conversely, sampling density had less effect on time to detection in high-virulent scenarios than in low-virulent scenarios (Fig. 7a). The influence of virulence on spread beyond the vineyard was similar to its influence on spread within the vineyard. Spread beyond the vineyard with heterogeneous soils was greater in low-virulent scenarios than in high-virulent scenarios; this difference was evident for homogeneous soils also and is likely linked to the time of detection (Fig. 5).

4 DISCUSSION

Our spread and surveillance simulations for radicicole phylloxera show that targeting surveillance strategies based on local-scale environmental spatial heterogeneity can decrease time to detection without increasing survey cost. Specifically, surveillance that targets soil that is more suitable for the invading organism is the most efficient strategy for detecting a new incursion. Increasing sample density also results in the earlier detection of an incursion but is little or no more effective than redistributing the same number of samples to target suitable soil. Increasing sample density requires greater resources and associated costs compared with the current and targeted suitable soil strategies. Therefore, as Epanchin-Niell *et al.*[6] determined at a landscape scale, we also suggest that accounting for spatial heterogeneity when designing surveillance strategies at local, field scales has the potential to improve surveillance efficiency and efficacy, and efforts should be made to obtain habitat suitability information for the species or vectors of interest, where possible.

As expected, increasing sampling density increased surveillance efficacy, and decreasing sampling density decreased surveillance efficacy in all scenarios and for all measures. However, the improvements in efficacy gained from each increment in sampling density were not particularly striking. Nonetheless, when we compare outcomes for the highest and lowest densities (which had a four-fold difference in density), we see that the differences in outcomes are significant. Therefore, as suggested previously, increased survey density may be appropriate for high-virulent genotypes that spread quickly to decrease their spread and establishment.[6] However, to properly address the question of the optimal surveillance density, a detailed economic analysis would be required, weighing the costs of increased sampling density against the value of the improved detection outcomes that our results show. This may be a valuable procedure, because spread rate and pattern were identified as the most important attributes to optimal surveillance from an economic perspective.[39] Additionally, in light of our results on targeted surveillance, any such analysis of increasing sampling

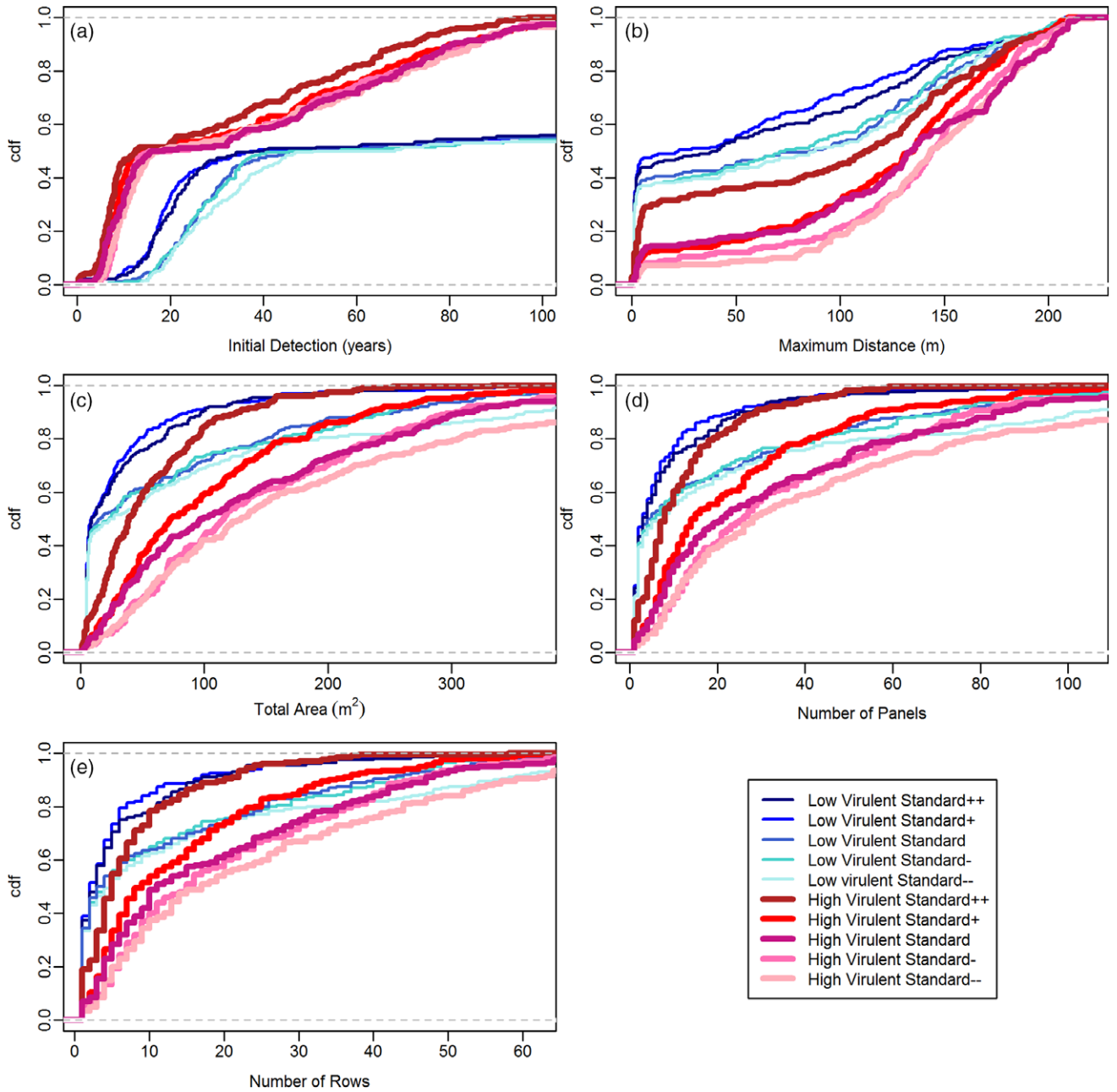

Figure 6. Results for all surveillance methods that vary the density of samples as variations on the standard in a landscape with 50:50 high : low soil suitability and 0.75 detection probability. The plots show the realized cumulative distribution function (cdf), with the *y*-axis indicating the cumulative probability. Initial detection time is represented by the number of years until the first detection occurs (a). The values for maximum distance travelled (b), total area infested (i.e. the number of cells that were infested) (c), and the number of panels (d) and rows infested (e) were all calculated at the initial detection time. The density of samples is indicated by density per ha compared with the standard ($n = 40$), standard^{+} ($n = 61$), standard^{++} ($n = 92$), standard^{-} ($n = 30$) and standard^{--} ($n = 23$). Lines that are further to the left indicate better surveillance outcomes (smaller time or spread for a given probability).

density should also consider targeted surveillance strategies, in situations where spatially heterogeneity is relevant.

Surveillance outcomes were highly influenced by the phylloxera virulence level, which represented differences in overall growth and spread rates as influenced by factors such as the virulence level of the phylloxera, grapevine root susceptibility and climatic and environmental suitability. In a heterogeneous environment, the incursion was often not detected within 100 years in low-virulent scenarios, indicating that surveillance may have limited success when invading phylloxera genotypes have low virulence, vines or rootstocks are highly resistant, and/or weather or soil conditions are not conducive to fast growth and spread (unless surveillance density and frequency were increased greatly). Incursions in high-virulent scenarios were likely to be detected earlier than in low-virulent scenarios, regardless of soil or surveillance strategy, because of their faster spread. In heterogeneous soils, the extent of spread within the vineyard at time of detection was lower in low-virulent scenarios than in high-virulent scenarios. This indicates that the longer time to detection in low-virulent scenarios may be offset because phylloxera will not have spread as far as

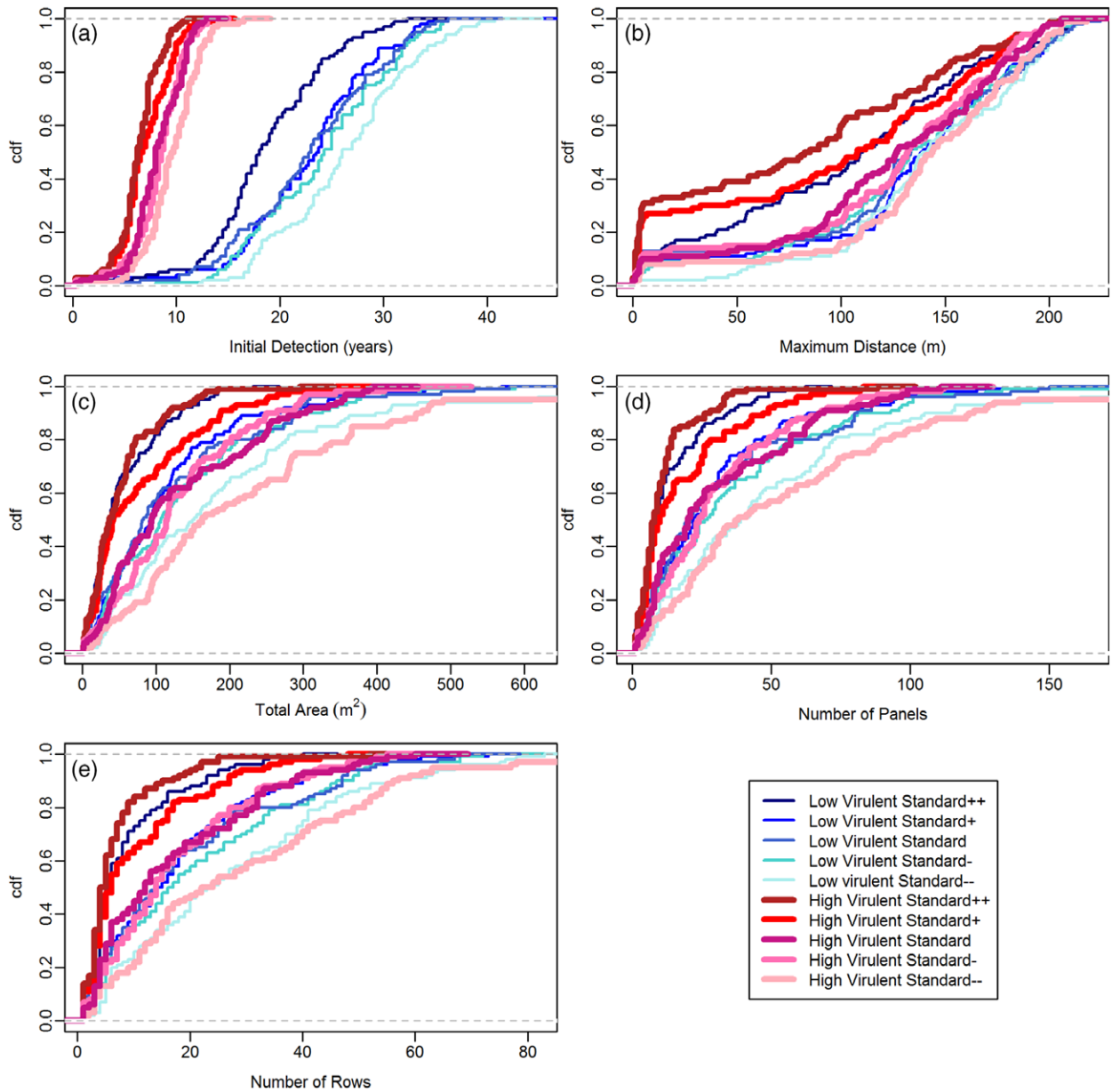

Figure 7. Results for all surveillance methods that vary the density of samples with variations on the standard strategy in a landscape with 100:0 high : low suitability soil and 0.75 detection probability. The plots show the realized cumulative distribution function (cdf), with the *y*-axis indicating the cumulative probability. Initial detection time is represented by the number of years until the first detection occurs (a). Values for maximum distance travelled (b), total area infested (i.e. number of cells that were infested) (c), and number of panels (d) and rows infested (e) were all calculated at the initial detection time. The density of samples is indicated by the density per ha compared with the standard ($n = 40$), standard^{+} ($n = 61$), standard^{++} ($n = 92$), standard^{-} ($n = 30$) and standard^{--} ($n = 23$). Lines that are further to the left indicate better surveillance outcomes (smaller time or spread for a given probability).

in the high-virulent scenarios. In homogeneous soils, differences in final spread outcomes due to differences in virulence were less clear; indicating that the faster spread in high-virulent scenarios is more or less equally offset by quicker detection. Varying sampling density had more effect on time to detection in low-virulent scenarios because the faster spread in high-virulent scenarios reaches sampling points more quickly and more consistently. The fact that there were much larger differences in spread measures in high-virulent scenarios in homogeneous soils is because the extent of spread is basically a product of time to detection and spread rates, and the greater spread rates in high-virulent scenarios more than offset the smaller differences in detection time. In particular, increasing sampling density had little effect on time to detection, but a larger effect on within- and beyond-vineyard spread measures. The initial location of an incursion is impossible to predict, but our results suggest that targeted sampling in high-suitability soil leads to increased detectability regardless of where the incursion begins – if the incursion reaches the high-suitability soil. However, if the incursion does not reach the high-suitability soil it is less likely that it will be detected (with current surveillance strategies or if it is unable to establish). In future, this model could potentially be used to retrospectively infer the initial point of infection or the actual importance of different factors in causing spread by comparing real and simulated patterns of phylloxera spread, thereby leading to improved surveillance designs.

Probably the most important measure of a biosecurity surveillance strategy is its ability to detect a new incursion at a given location before it has spread to further new locations. In this case, this means minimizing the number of phylloxera that move out of the simulated area before detection occurs, whether carried by humans, machinery or wind (phylloxera never moved beyond the simulated area due to their own short-range diffusive movement). While early detection likely results in decreased potential for an incursion to spread to another block or region, initial incursions typically include few individuals and thus early detection is not always likely or possible.[8] This is evident in our results where, although early detection was important in reducing onward spread, no surveillance strategy resulted in the incursion always being detected while it was contained within a block. For both high- and low-virulent scenarios, and both soil types, the incursion had the potential to spread to new blocks and regions, regardless of the surveillance strategy. The potential of spread to these new areas was dependent on vector movement, and although movement via wind was restricted with the presence of a 65 m buffer, the potential for movement via machinery and human vectors to new blocks and regions was high. This highlights the importance of implementing strict hygiene procedures designed to decrease movement via machinery and human vectors even when the status (invaded/not invaded) of the block is unknown. Often hygiene protocols are clearly defined, but incursions continue to occur[12,15] suggesting there is either a lack of implementation or efficacy of protocols.[40,41]

The spread of invasive species is influenced by many factors including population dynamics, vector dispersal, biotic and abiotic factors, and landscape heterogeneity.[42–44] Our model simplifies many of these complexities and although we have used published literature and expert advice to inform our models and make them as realistic as possible, we recognize that models can never perfectly predict what will happen in the field. In particular, as more data become available on soil and phylloxera genotype interactions, and temperature and phylloxera genotype interactions, the model could be refined to better address the influences of climate and soil attributes on phylloxera genotypes. Recent studies have highlighted that temperature has a significant impact on the survival of different phylloxera strains.[40] Additionally, our simulations assume that a pest is detected at a set detection probability; however, we acknowledge that sampling effort, expertise, method and timing will also likely impact the probability of detection[45] and note that the variance of the model predictions will increase and decrease with low and high detection probabilities, respectively.[46] Accounting for property history (e.g. absence of hygiene compliance or shared machinery with other properties) or incorporating visual assessments of plant health by experts may also improve surveillance.[47] However, visual assessment relies on symptoms that are often not evident until many years after the initial incursion, and thus the pest will have likely spread to other fields or regions. Other methods such as ground or aerial surveys (e.g. hyperspectral leaf-level reflectance spectrometry, multispectral images or electroconductivity: EM38)[10,48,49] are likely to have similar limitations. Basing surveillance on a history of poor hygiene compliance or machinery sharing by an infested block or property is also likely to be of limited help in reducing onward spread unless the poor hygiene compliance or machinery sharing can be recognized and acted on almost immediately. Therefore, effective proactive surveillance, incorporating local-scale spatial heterogeneity where appropriate, aimed at identifying pests as early as possible is essential.

Two pre-emptive strategies previously proposed to reduce the risk of incursion or slow the spread of grape phylloxera are: (i) planting resistant grafted grapevines, and (ii) enforcing strict quarantine zones and using effective disinfestation procedures for vectors likely to increase the risk of phylloxera spread.[12,32,40,41] Our results suggest that although resistant grafted grapevines will reduce the economic impacts of a phylloxera incursion and reduce the rate of spread (due to lower abundance of high-virulent strains; low-virulent strains may occur in greater abundance on rootstocks), they will probably not reduce its onward spread and may actually exacerbate it due to much slower rates of detection and a higher rate of complacency. Moreover, a combination of effective buffer zones around blocks, effective hygiene procedures and proactive surveillance are also required to significantly reduce the risk of further onward phylloxera spread. For hygiene procedures to be effective, they would need to be enforced and strong evidence and effective education presented to growers to encourage voluntary compliance. Furthermore, accounting for spatial heterogeneity in designing surveillance strategies could significantly increase their effectiveness and reduce the associated economic and labour costs. EM38 surveys can be used to collect data that captures spatial differences in soil suitability and this can then be mapped.[10,13] Surveillance strategies could then be designed using these maps to target hot spots for enhanced surveillance. Vineyard managers are already encouraged to collect EM38 data for other aspects of grapevine production, so there should be little increased cost.[50] Several new methods for early phylloxera detection are currently being developed and trialled, including chemical and pigment fingerprinting of metabolites as biomarkers in leaves,[21,51–53] a phylloxera-specific DNA probe,[54,55] emergence traps[15,56] and, more recently, the use of unmanned aerial vehicles[57] and sniffer dogs.[58] The efficiency of all these new methods has the potential to be improved by spatially targeted surveillance designs like those considered in this study.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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