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Surveillance to Inform Control of Emerging Plant Diseases: An Epidemiological Perspective

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Abstract

The rise in emerging pathogens and strains has led to increased calls for more effective surveillance in plant health. We show how epidemiological insights about the dynamics of disease spread can improve the targeting of when and where to sample. We outline some relatively simple but powerful statistical approaches to inform surveillance and describe how they can be adapted to include epidemiological information. This enables us to address questions such as: Following the first report of an invading pathogen, what is the likely incidence of disease? If no cases of disease have been found, how certain can we be that the disease was not simply missed by chance? We illustrate the use of spatially explicit stochastic models to optimize targeting of surveillance and control resources. Finally, we discuss how modern detection and diagnostic technologies as well as information from passive surveillance networks (e.g., citizen science) can be integrated into surveillance strategies.

INTRODUCTION

Emerging diseases: infectious diseases that appear in a population for the first time or suddenly increase in incidence

Surveillance: an official process that collects and records data on pest or pathogen occurrence or absence by survey, monitoring, or other procedures

Epidemic: increase in the amount of an infectious disease in space and/or time

Recent times have seen a dramatic rise in the number of emerging diseases of plants associated with a range of natural and anthropogenic factors. Pathogens have been introduced to new geographic areas by human movement of infected material (17), long-range wind dispersal of inoculum, and changes in climate that favor pathogen establishment in areas where it was not possible before (106, 118). New strains of pathogens have also emerged to overcome previously effective disease control methods and unfavorable environmental conditions (120). The impacts on crop production and food security have been extreme. Prominent examples include Ug99 and other novel strains of wheat stem rust in Africa and the Middle East (119, 120), citrus canker (48) and citrus Huanglongbing (29, 47) in North and South America, cassava diseases in Southeast Asia and East Africa (52, 73), and race TR4 of Panama disease on Cavendish bananas in Asia (94). Natural environments are also under threat (40), for example, by arboreal diseases, such as ash dieback (caused by *Hymenoscyphus fraxineus*) (133) and sudden oak death (caused by *Phytophthora ramorum*), which have led to significant damage to forest ecosystems in Europe and the United States, respectively (53). The recent arrival of *Xylella fastidiosa* in Europe serves as a particularly stark reminder of the danger posed by emerging plant diseases (84). The subspecies *pauca* of *X. fastidiosa* was discovered on olive trees in Apulia, Italy, in 2013 and has spread throughout the local region (84) with far reaching economic and social impacts in an area where this ancient crop is an established part of the heritage (84). The long list of potential host species for *X. fastidiosa* means that this pathogen is a considerable threat throughout Europe, and more recent detections of *X. fastidiosa* in France and Spain demonstrate the potential for further pathogen spread (5).

Surveillance involves the collection and analysis of information relating to plant disease epidemics and is crucial for detection and successful control of emerging pathogens and strains. Consequently, there have been renewed calls for improved surveillance strategies across plant health (8, 33, 85, 107). Formal horizon scanning (114) and international networks of plant sentinels (6) serve to anticipate new threats, and improved use of quarantine and border inspections can reduce the risk of entry to new areas (85). However, preemptive measures such as these cannot avert all epidemics. Post-border invasion of disease is inevitable and necessitates surveillance within agricultural landscapes and natural plant communities. The challenges of early detection and assessment of invasion are substantial for plant disease. Epidemics are frequently initiated and spread through vast, often heterogeneous, landscapes of interconnected host populations driven by highly variable natural and human-mediated dispersal mechanisms. Whereas surveillance is commonly augmented for human and livestock disease through self-reporting by patients and animal owners, this is seldom the case for plant disease. The problems of detecting early infections or even the spread of an establishing epidemic are compounded by the cryptic nature of many plant diseases. Infectious hosts or indeed whole plantings may go undetected while providing a source of inoculum for spread ahead of visible epidemic fronts. The motivation in writing this review is to show how epidemiological insights into the dynamics of disease spread can be used to improve the effectiveness of disease surveillance strategies for emerging epidemics.

The consequences of failure to implement effective surveillance programs can be severe. Despite its steady advance across Europe, ash dieback was not discovered in the United Kingdom until 2013, by which time it was already widespread (133). New foci of *X. fastidiosa* continue to emerge in unexpected places in Europe beyond areas of intensified surveillance (84). Late discovery of new epidemics limits the feasibility of eradication efforts and facilitates onward spread to new areas. Recent work by Cunniffe et al. (26) has shown, for example, that it could have been possible to restrict the spread of sudden oak death in California had appropriate (albeit costly) steps been undertaken early enough based on surveillance data and knowledge of the epidemiology

of *P. ramorum*. Meanwhile, insufficient gathering of epidemiological information undermines our ability to predict major epidemics accurately (125) and leads to ill-informed interventions. The challenges are exacerbated for plant health practitioners who often deal with multiple simultaneous threats under time-sensitive conditions and with limited budgets for surveillance and control. Improving the efficiency and cost-effectiveness of surveillance strategies for emerging plant diseases is accordingly an important contemporary challenge in plant health.

Incidence: the proportion of diseased individuals in a population (synonymous with the term "prevalence" as it is used in human and animal epidemiology)

The heterogeneous distribution of disease across plantings, forests, and landscapes requires careful thought on how surveillance is conducted. Indeed, although surveillance is defined as "an official process that collects and records data on pest occurrence or absence" (38, p. 16), in practice many surveillance programs are ill-informed by or ignore the processes that actually determine the dynamics of disease spread. However, knowledge of disease dynamics should make it possible to know when and where a pathogen is most likely to occur. In this review, we explore how epidemiological information about disease spread can be used to inform and adjust surveillance strategies for cost-effective control of emerging plant diseases. We include epidemiological realism by accounting for the dispersal and transmission of pathogens, which are constrained by the host population. We approach this by first looking at relatively simple statistical descriptions of surveillance and then proceed to more mechanistic epidemiological models that make use of enhanced computer power. Although surveillance planning and evaluation are traditionally focused on official or regulatory surveys conducted by trained surveillance operatives, new information sources, which we also explore, are increasingly available. For example, citizen science initiatives (15, 19, 25, 32, 34, 43, 56, 62, 68, 82, 89, 108), as well as reports from growers and landowners, have been enabled by smartphone technology (32) and increasingly user-friendly diagnostics (31).

PLANT DISEASE EPIDEMIOLOGY AND SURVEILLANCE

Clarifying the Objectives for Surveillance

Surveillance is conducted for a range of objectives (9). Optimal allocation of resources for surveillance requires adjustment of surveillance strategies according to the specific objective. Considerable effort has been put into understanding endemic disease where the surveillance objective is primarily to understand how much is present (11, 79, 81). In this review, we focus on emerging epidemics, in which a pathogen arrives and spreads rapidly through a new geographic area.

For emerging disease, surveillance is generally conducted for three broad objectives: detection, estimation, and targeting. We need to know whether a pathogen or strain is present (detection), gather information to understand the nature and extent of the problem (estimation), and, finally, identify as many infected sites as possible to implement control (targeting). The first of these objectives involves the question of whether or not the pathogen, and hence the disease, has arrived in a given area. It is imperative to detect infection as early as possible so that appropriate control or eradication efforts can be implemented (26, 98, 128). Conversely, if no cases of infection are found, a question naturally arises: Is disease absent or did it go undetected by chance or due to the use of an imperfect test (20, 55)? The second objective, estimation, follows the discovery of a new disease and concerns how much is present and where the disease is located, i.e., the incidence and distribution of the pathogen or strain. We may also wish to know how fast the epidemic is spreading and what environmental or other factors such as trade are driving spread. Finally, targeted surveillance (102) aimed at maximizing detections of new cases is required to implement control or eradication, for which we need to discover new foci as well as delimit existing foci (e.g., 30).

In order to design an effective surveillance strategy for a particular objective, we need to understand when, where, and how disease is likely to occur and at what intensity. Crucially, this

information is used to identify how many sites should be surveyed, how often, and where. We can begin to do this with standard statistical approaches that use probability distributions to capture the intensity and variability of disease and relate this to sampling effort. In the following section, we illustrate some elementary yet powerful statistical approaches to specify the sampling effort required to achieve particular levels of confidence in a surveillance plan. The statistical approaches involve certain simplifying assumptions about epidemic dynamics. We explore how relaxing some of these assumptions to allow for temporal and spatial dynamics of epidemics can improve the flexibility of the statistical approach. This leads naturally to consideration of the use of spatially explicit stochastic simulation models to inform surveillance schemes by simulating the dynamics of emerging epidemics across heterogeneous landscapes under varying environmental conditions.

Statistical Approaches to Surveillance

International guidelines emphasize the importance of statistical methods to inform surveillance (37). In plant health, this has largely focused on the application of statistical modeling methods drawn on binomial sampling theory and related probability distributions (76–79). Originally developed with endemic disease in mind, these methods are frequently used to estimate the incidence of endemic disease, for example, to assess whether a disease has exceeded a threshold level beyond which a disease management decision is made (21) or to determine the number of samples needed for accurate disease estimation (how many samples should I take to estimate disease within ± 10%?) (57, 81). Here, we focus on methods to improve the effectiveness of first detection, which, until recently, has received little attention. The number of samples required to detect a disease below a given incidence can be straightforwardly calculated from the binomial distribution. That is, the probability (P) to detect at least one case of disease with sample size N and true disease incidence q is

$$P = 1 - (1 - q)^N. \qquad 1.$$

Suppose the incidence of a disease is $q = 0.01$ (i.e., 1% of the population is infected), then 300 samples would be required to have a 95% probability of detecting at least one infected host. To detect even earlier, e.g., before the epidemic reached 0.1%, would require at least 3,000 samples. The expression (Equation 1) makes a number of simplifying assumptions, not least that samples are randomly drawn from an infinitely large population using a test with perfect sensitivity, but it serves as the underlying probability model from which more realistic forms can be derived. Related calculations can be performed. For example, if disease has not been found in a preliminary survey, what is the probability that disease is present but was missed by the survey simply owing to chance (20)? This is an important practical issue in plant health that underpins evidence to support claims of pest-free areas (116). Statistical approaches to these questions of the probability of freedom from disease given a survey are well established in the field of animal health (13, 20, 83, 131), but they deserve more attention in plant health (55). Although surveys that discover no cases of disease are commonly interpreted as confirmation of absence, it is impossible to state with 100% confidence that disease is really not present unless all host tissue is sampled and the test sensitivity is perfect. However, if there is no evidence of infection in any of the samples, it is possible to infer the probability that the true incidence is below a certain threshold, based on the sample size. To do this, q in Equation 1, which is known as the design prevalence, is set to an acceptable threshold level for infected individuals in the population, below which it is acceptable to declare "freedom" from the pathogen. This approach can also be used for survey design by reformulating Equation 1 to estimate the sample size required to achieve a given level of confidence. For highly sensitive diagnostic tests, the so-called rule-of-three approximation (64, 65, 81, 117) can be used to identify

with 95% confidence the maximum incidence of disease in the population given that no disease is found in N samples:

$$q^* = \frac{3}{N}.$$

The rule-of-three approximation provides a quick and easy means to assess the confidence that can be placed on survey results reporting freedom from disease. For example, if 100 trees were randomly inspected from a population of 1,000 trees and none tested positive, there could be as many as 30 infected trees (0.03 as a proportion) that were missed by chance (and that could pose a significant threat). Statistical approaches to surveillance have also been adapted to incorporate some epidemiological characteristics of disease, for example, through the use of the beta-binomial distribution to account for the level of expected spatial clustering of disease and its impact on estimates of incidence from a sample (58–60, 69, 77–80, 127).

The strength of these approaches is that they provide users with a simple means to relate the incidence of disease with sampling effort and thus the ability to make inferences about how much sampling effort is enough and what the sample tells us about the epidemic. Even so, statistical approaches tend to treat epidemics as though they were static and seldom account for the dynamics of an epidemic or include a mechanistic understanding of how disease spreads.

Accounting for Temporal Dynamics

Key characteristics of an emerging epidemic are its pattern and rate of spread. Building on the use of statistical methods to address the objective of detection, recent approaches have been developed to extend binomial sampling methods to incorporate more epidemiological features of emerging diseases. This can be done by linking statistical models of sampling with epidemiological models of the transmission of infection (1, 2, 98, 99). For example, Parnell et al. (98, 99) developed a simple rule of thumb approach to address the following question: Given that a surveillance program is in place, what incidence will an epidemic have reached when it is first discovered (**Figure 1**)? Usually, early detection surveillance programs consist of multiple rounds of survey, during which the epidemic may arrive and begin to spread. The incidence of disease therefore changes and so does the probability of detection. For epidemics during the early stages of spread, in areas where susceptible hosts are not limiting, the rate of spread can be approximated by an exponential function. The probability of detecting an epidemic is thus a function of sampling intensity but also the rate at which the epidemic is spreading (**Figure 1**) (2, 98, 99). Parnell et al. (98) found that the mean incidence an invading epidemic will have reached when it is first discovered can be calculated from the rule of thumb

$$E(q^*) = \frac{r\Delta}{N} = \frac{rate\ of\ epidemic\ increase}{rate\ of\ sampling}, \qquad 2.$$

where r is the rate of initial epidemic increase, Δ is the time interval between rounds of sampling, and N is the number of samples taken per round (and hence N/Δ is the rate of sampling). The rule of thumb (Equation 2) has been validated and shown to be robust to real epidemic data, supporting the view that simple equations can be put to powerful use to support early detection surveillance (98). In general, epidemics characterized by faster rates of growth require increased surveillance effort (in terms of sample size and sampling frequency) than those with slower rates of growth. Growth rates of ash dieback disease in experimental plots have been estimated at 0.0026 per day (2). This indicates that if 30 plants were sampled every three months (90 days), an invading epidemic would be discovered on average when it had reached 0.8% incidence in the population. In contrast, epidemics of citrus Huanglongbing in Florida can have growth rates of up to 0.0143 per day in

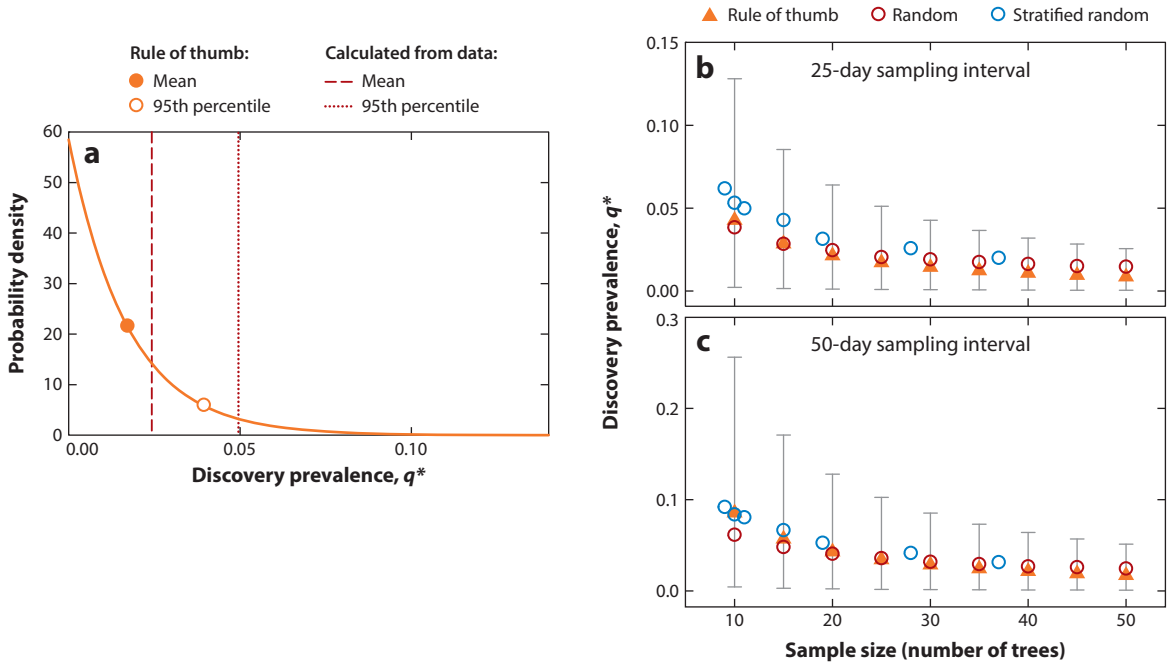

Figure 1

Linking statistical and epidemiological models; the robustness of a rule of thumb (Equation 2) to determine the prevalence (a.k.a. incidence) of an emerging epidemic when it is first discovered (i.e., discovery prevalence) (98). Shown are discovery prevalences for an epidemic of citrus canker disease in urban Miami. (*a*) The distribution of discovery prevalences for sample size, *N*, of 50 trees and sample interval, Δ, of 50 days. The mean and 95th percentile discovery prevalences are shown for the rule of thumb (*solid* and *open circles*, respectively), and the dashed and dotted lines denote those prevalences calculated by simulating a sampling plan on the real epidemic data from Miami. (*b*,*c*) The change in discovery prevalence with sample size, *N*. Shown are the mean discovery prevalence from the rule of thumb (*orange triangle*) and its 90% confidence interval (5th and 95th percentiles), and the mean discovery prevalence using simple random sampling (*red circles*) and stratified random sampling (*blue circles*) for sampling intervals of (*b*) 25 days and (*c*) 50 days. Adapted from Reference 98.

young plantings (98). A similar surveillance regime (30 trees every 90 days) would allow the epidemic to reach nearly 4.3% incidence on average before first discovery. Approaches for other types of invasive species have also explored how temporal dynamics can be incorporated (18, 74). Note that, thus far, we have largely assumed that it is possible to quantify the survey effort for official surveys carried out by experienced personnel. Determining survey effort from detections made via citizen science initiatives, or other types of passive surveillance (56), is more challenging, largely because absence data are usually not recorded (only positives). However, proxy methods to estimate absence data may be possible. For example, Pocock et al. (109) used routine observations of native moths as a proxy for survey effort for rarer detections of the oak processionary moth.

Cryptic infection: infection caused by a pathogen in a plant or patch of host that is not detectable

Passive surveillance: reporting of disease by citizens, growers, or the community; not linked to official surveys

Cryptic infection, during which an infectious host is asymptomatic, can also be accounted for (1). Whereas some pathogens have short cryptic periods, others can be infected but remain asymptomatic for several years. Citrus Huanglongbing has a variable cryptic period that can be up to three years (47, 104). By contrast, *P. ramorum* typically expresses symptoms within four weeks of infection (2). The probability of detecting disease in surveillance programs that are based on visual inspection is therefore clearly influenced by the time taken for symptom expression. Alonso Chavez et al. (1, 2) showed how the increase in asymptomatic infection is related to the

increase in symptomatic, detectable disease and thus factored cryptic infection into the design of surveillance programs. In extreme cases, visual inspection may be insufficient to detect disease before a high level of infection has occurred (1). Indeed, a recent study of citrus Huanglongbing disease suggested that all trees within a plantation could be infected within a year, before any symptoms manifest (72). Modern diagnostic and detection methods (85, 86, 93) offer considerable potential to detect cryptic spread with ever more sensitive, mobile, and rapid technologies. To do so, they must be used not only to confirm visual symptoms but also to sample seemingly asymptomatic plants. The sensitivity of such methods can be captured by the statistical framework discussed here and used to give due consideration to sampling effort and timing. Remote-sensing technologies are developing quickly and have shown potential for identifying infection over large spatial areas with reasonable accuracy (e.g., 134). However, the ability to detect emerging cryptic infection during the early stages of emerging disease spread, when incidence is still low using these methods, is not clear and thus still relies on inspection and sampling of host tissue.

Disease risk: the product of the consequences of an infection and the probability of that infection occurring

Accounting for the Spatial Distribution of Disease: Geostatistical and Niche Models

As well as accounting for when an epidemic occurs and how fast it might spread, we also wish to identify how the risk of disease varies across a susceptible landscape. Estimating the spatial distribution of an emerging epidemic is crucial to enable understanding of how it spreads over time, especially through complex host landscapes, and where disease control efforts should be prioritized. There have been two main statistical approaches of relevance to plant health: geostatistics (16, 23, 41, 42, 122, 123, 126, 129) and the use of species distribution or niche models (87, 111, 128).

Geostatistical methods can be used to make inferences on the spatial distribution of disease throughout an area of interest following initial subsampling of the area (16, 42, 63, 70, 71, 95, 105, 113, 123, 126). The method involves fitting a statistical relationship to predict a surface of disease incidence, or other measure of disease occurrence, from the initial set of point samples. However, by not capturing the epidemiological processes involved in transmission and spread, geostatistical approaches, of which kriging is a typical example, can lead to overestimation of disease risk when they fail to account for the patchy nature of host distributions and the limiting effect this can have on epidemic spread (75, 101). Although approaches such as co-kriging and regression kriging (e.g., 16) have been applied to account for host variability, they are static in nature and do not yet fully account for the effect of, for example, landscape connectivity on spread.

Species distribution and niche modeling capture the impact of spatially varying environmental conditions (e.g., 87, 90, 128). These methods combine data on the presence and absence of a target species, such as pests or pathogens, with environmental predictors of suitability to estimate maps of where a species is likely to occur. However, a challenge related to their application, particularly to emerging plant diseases, lies in the implicit assumption that the species under analysis is in equilibrium and all locations have an equal chance to become infected, i.e., have all been challenged with inoculum, although some studies have partly overcome this by including pathogen dispersal constraints (128).

Arguably, none of the elaborations for kriging or niche modeling fully account for the connectedness of the host landscape and the impact that connectedness and discontinuities of susceptible host populations have on disease dynamics and the rate and direction of pathogen spread.

Using Risk-Based Assessments to Inform Surveillance

Parnell et al. (102) demonstrated a pathogen-generic framework to determine spatial estimates of risk for emerging plant disease, which includes mechanistic epidemiological understanding, and

showed how this could be used to determine risk-based surveillance plans. Risk at any location in a map is defined as the product of (*a*) the basic reproductive number, R_0, at that location and (*b*) the probability that a particular location becomes infected. It therefore incorporates both the potential distribution of a disease (i.e., through the basic reproduction number) and its likely dispersal from known infection locations. One way to prioritize a survey based on assumed risk is to conduct a weighted random sample, i.e., weighted toward the highest risk locations. Using citrus Huanglongbing in Florida as a retrospective test example, Parnell et al. (102) showed that, even when only utilizing minimal available epidemiological information (such as the age of citrus plantings and the association of younger plantings with higher infection rates) and the results of a single survey of disease distribution, the approach significantly outperformed uninformed survey methods (e.g., simple random sampling) (102). The result demonstrates how even basic epidemiological information can be of value for surveillance planning. This is particularly significant because targeting surveillance effort toward sites at higher risk of infection can improve the efficiency of early detection surveillance. The risk-based survey method has been adopted by USDA-APHIS (US Department of Agriculture–US Animal and Plant Health Inspection Service) since 2006 and has since been further developed and applied to other epidemics, including citrus Huanglongbing in California, Texas, and Arizona (49, 50) and *Plum pox virus* in New York State (51). Similar benefits for pathogen detection for risk-targeted surveillance schemes have also been demonstrated in livestock disease systems (e.g., 54).

Risk-based surveillance: targeting of surveillance based on disease risk

Basic reproductive number: the average number of cases one infected case generates over its infectious period in an otherwise uninfected population

These approaches to capture spatial information on disease presence and risk are of significant utility for improved surveillance and control of emerging diseases. They are static in nature and of particular use when data on disease progress over multiple time shots are not available. In the next section, we explore spatial approaches that explicitly account for both temporal and spatial dynamics of epidemics and the availability of susceptible hosts.

SPATIALLY EXPLICIT SPREAD MODELS TO INFORM SURVEILLANCE AND CONTROL

Recent advances in computational power enable the use of stochastic spatially explicit models of epidemics to simulate realistic patterns of epidemic spread through landscapes (27, 28, 39, 46, 61, 92, 100, 103, 104, 112, 121, 124, 130). These models are used to predict where the pathogen is most likely to spread across heterogeneous landscapes, allowing for inherent variability in pathogen transmission, fluctuating environmental conditions, discontinuous host distribution, and uncertainties in the current levels of knowledge about the pathosystem (46). The models are also designed to compare the effectiveness of different disease management scenarios. Here, after a brief review of the flexibility of compartmental epidemiological models to monitor and predict the temporal and spatial dynamics of emerging epidemics, we consider current challenges in using model-based strategies for optimal surveillance and control.

The Structure of Spatially Explicit Stochastic Epidemic Spread Models

A common class of spatially explicit stochastic models involves variants of the SIR (susceptible, infected, removed) epidemiological model widely used in human epidemiology. The models are flexible in capturing a range of mechanisms, including host connectivity and fluctuating environmental conditions. The models keep track of how the disease status of each individual host unit in a population changes over time according to whether an individual is healthy (i.e., susceptible), infected, or removed (i.e., no longer infectious, which includes recovered individuals, for example, after chemical treatment as well as dead individuals). An individual could be a plant, but it may

be an entire field, plantation, or forest, depending on the spatial scale of interest. The host distribution can be represented as point processes (28, 100, 103), as nodes in a commercial network (4, 22), or, more commonly, as a rasterized landscape comprising contiguous cells in which the proportion of susceptible hosts within cells is known or estimated (26, 88). The models can be simplified, losing a term, to give an SI (susceptible-infected) model in which there is no recovery or death. Terms may also be added, as in the SECIR forms, to distinguish latently infected (E, exposed but not yet infectious), cryptic (C, infectious but not yet symptomatic), and infectious (I) hosts (26, 46). Stochastic transitions occur between each successive class governed by contact and transition probabilities that may be weather driven. Infection of susceptible hosts is determined by a transmission rate and a dispersal kernel to account for the falloff in the probability of inoculum reaching more distant hosts.

Surveillance for Parameter Estimation to Characterize Epidemic Spread

There is usually little prior knowledge to predict the spread of emerging epidemics in a new region. Surveillance plays an important role in the parameterization and design of predictive models for emerging epidemics. Models are usually parameterized using Bayesian or other computationally intensive methods to infer transmission and dispersal rates from successive snapshots of disease, which are derived from repeated surveys (24, 97, 104). A detailed explanation of stochastic SECIR models and how observational data can be used for model parameterization is provided by Gibson et al. (45) and Gibson & Gilligan (44). Although, in principle, it is possible to estimate dispersal parameters from a single snapshot (66), in practice that can be done only under restrictive assumptions for a system in equilibrium. Therefore, the more snapshots that are available, the better the chance is of successfully parameterizing the models. This leads naturally to the simple question of how many snapshots are sufficient for the purpose of predicting future spread of an emerging epidemic. Baxter & Possingham (7) have shown that more time spent gathering information on the spread of invading species can lead to more effective interventions in the long run. However, there is a trade-off: Waiting too long to accumulate more information may mean the epidemic has spread so rapidly and so far that it can no longer be effectively controlled (26, 28).

Using Asiatic citrus canker in Miami as a case study, Neri et al. (97) examined the value of taking different numbers of successive snapshots (cumulative time windows) and starting at different times (sliding time windows) at one or more discrete locations through Miami (**Figure 2**). Neri et al. (97) used Markov chain Monte Carlo Bayesian methods to estimate dispersal kernels and rates of primary and secondary transmission for Asiatic citrus canker spreading through urban populations of trees. Parameter estimates were consistent across different locations, indicating that surveillance at multiple independent sites was not essential. However, successive snapshots for a given site (comprising multiple urban blocks) greatly improved estimation, measured by the width of posterior distributions of parameters (**Figure 2*a–c***) and the predicted distributions for the range of possible outcomes from the point of prediction. Encouragingly, the dispersal scale of an invading epidemic (which plays a crucial role in the design of effective control strategies) could be accurately characterized from relatively few snapshots (**Figure 2*a*,*d***), even when observations began after the epidemic had passed its early stages of development (later sliding windows) (97). The dispersal scale plays a crucial role in the design of effective control strategies, and many emerging diseases are not discovered until they are already past the early establishment phase. The result requires testing for other host-pathogen systems to establish its generality. Prediction of the future course of the epidemic was confounded in this epidemic by the rate of secondary transmission slowing as conditions became abnormally dry, but this could be incorporated into the epidemic model to give an improved fit (97).

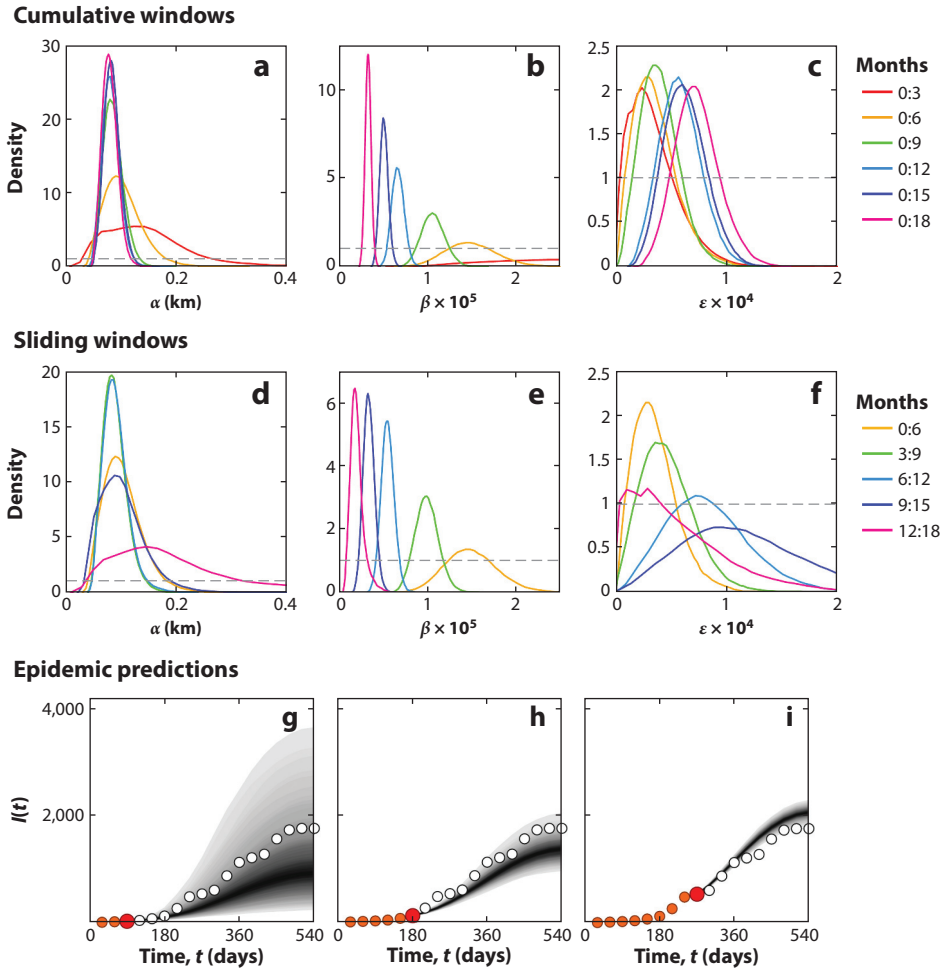

Figure 2

The accuracy of parameter estimates and the ability to predict epidemics depend on the amount and timing of epidemic data from surveillance (97). Surveillance involved successive, mapped snapshots of healthy and infected trees across an urban site with a total of >6,000 citrus trees. (*a–c*) Trends over time in the posterior densities for Bayesian Markov chain Monte Carlo estimation of (*a*) the dispersal scale (∝), (*b*) the secondary transmission rate (β), and (*c*) the primary infection rate (ε) for a model with an exponential dispersal kernel and external inoculum, based on cumulative windows that successively encompassed three additional monthly snapshots of data extending from 0–3 to 0–18 months. The gray dashed lines represent the prior distribution, rescaled for display by a factor of 10^5 for β and 10^4 for ε. (*d–f*) Corresponding trends in posterior densities for parameters based on sliding windows encompassing six successive months of observation beginning at 0, 3, 6, 9, and 12 months. The results show relatively rapid convergence for the dispersal scale. Estimates for β improved with additional observations (i.e., showed tighter posterior densities) but also decreased over time as conditions became drier. (*g–i*) Predictions of future disease based on observation windows of increasing length comprising data from the first (*g*) three, (*h*) six, and (*i*) nine snapshots of disease. The probability distributions for predicted trajectories are shown by gray shading, with intensity of shading representing probability of occurrence. The observational data (disease snapshots) used for prediction are marked by orange circles, the last snapshot used (the prediction time) is marked by a larger red circle, and the observational data to be predicted are marked by white circles. The predicted trajectories are derived by sampling parameters from the posterior densities at the time of prediction with the added assumption that β declines linearly with time. Abbreviation: *I*, number of infected trees. Adapted from Reference 97.

The design of surveillance schemes to estimate parameters for emerging epidemics is a challenging area of current study. Estimation is frequently confounded by incomplete and late reporting and by interference from ad hoc disease control activities during the early stages of an epidemic when parameters are being estimated. Parry et al. (104) showed how to account for interference caused by spraying for the vector of citrus Huanglongbing during data collection for parameter estimation. There is also a common tendency to collect samples close to where disease is already known to occur. The additional information provided by these samples is often negligibly small, especially in extracting spatial signals about dispersal. Isolated foci may arise from primary infection derived from inoculum sources outside the region of interest. New foci may also be an intrinsic feature of the dispersal process that can be captured by a power law, in which the probabilities of long-distance dispersal events are inflated compared with an exponential kernel characteristic of a spreading wave. The connectivity of hosts through the landscape also facilitates spread through multiple short-distance jumps across host stepping stones (90), enabling the epidemic to take an unexpected path through the landscape.

Some exploratory work has been done on the optimization of data collection to estimate parameters for temporal epidemic models (24) using ideas derived from optimal design theory for linear systems (3). Future work will extend these methods to improve the efficiency of data collection for parameterization of spatiotemporal models. There are natural pressures when dealing with emerging epidemics to target surveillance on locating positive sites at the expense of reporting negative sites, yet these data are essential to minimize overestimation of epidemic rates. Recent studies by Williams et al. (131, 132) in veterinary medicine have shown how the dual, and sometimes conflicting, surveillance objectives of estimation and targeted control can be resolved. More broadly, future developments in estimation will also benefit from advances in remote sensing (86), diagnostic networks (93), and citizen science (32) for detecting diseased and healthy hosts. Cryptic infection poses an additional challenge. Lee et al. (72) recently suggested that citrus Huanglongbing, which is transmitted by psyllids, can reach 100% incidence by the time the first symptomatic tree appears. Thompson et al. (125) have shown using models motivated for Ebola, a human disease, that the ability to forecast major epidemics is not possible without estimating the proportion of asymptomatically infected individuals in the population. The effective deployment of diagnostic methods to identify infection (85, 86) informed by model predictions about likely extents of cryptic infection is an important area of future research.

Model-Based Strategies for Optimal Surveillance and Control

Given a parameterized model, it is possible to infer the effectiveness of different surveillance and disease management scenarios (26, 98). Consider first when surveillance is required to report as many positive cases as possible without necessarily invoking control. Using a spatially explicit stochastic model for Asiatic citrus canker spread in Queensland, Potts et al. (110) showed how adaptive surveillance radii should be used to maximize detections of Asiatic citrus canker disease. The length of the search radius is a function of how long a location has been infected and thus how far the pathogen could have dispersed. Similar approaches could be used to ascertain disease absence (i.e., pest-free areas). Russell et al. (115) showed how spatial models could be used to optimize surveys to ascertain the absence of rodents after an eradication effort. The authors simulated the growth and dispersal of the rodent population and determined the optimal location for traps or other devices and the number of nights of monitoring required to infer eradication. The methods are adaptable for plant health and are likely to become more important as improved pathogen sensors are introduced (85, 86).

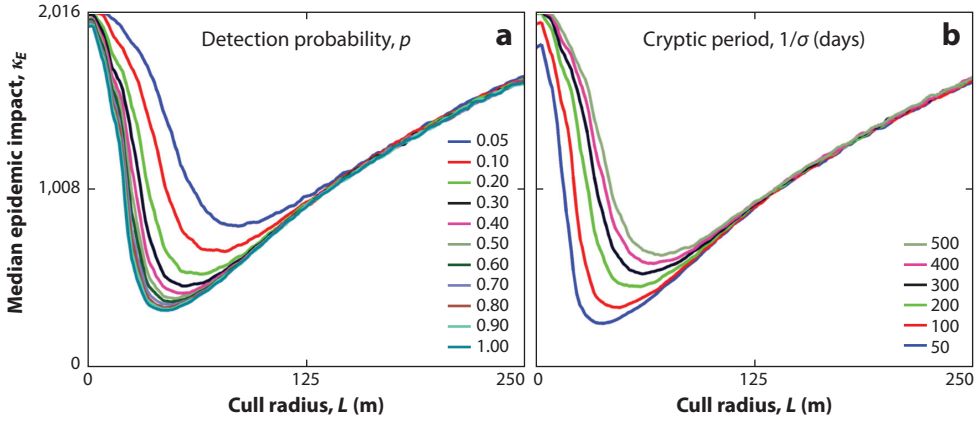

Figure 3

The effect of different detection probabilities and length of cryptic infection on the impact of epidemic control (28). The example shown is for the eradication of citrus Huanglongbing disease using a host cull radius around symptomatic plants. (*a*,*b*) Responses of the median epidemic impact (measured by the number of hosts lost to disease and healthy hosts removed by control) to cull radius for different values of the (*a*) probability of detection and (*b*) cryptic periods. The optimal culling radius increases as detection probabilities decrease and the cryptic period lengthens. Adapted from Reference 28.

Models can also be used to link surveillance explicitly with control strategies, for example, when each new detection event leads to an associated control action at that location, such as roguing infected hosts. In plant health, SECIR models have been successfully used to determine large-scale control strategies, including the deployment of genetic, chemical, and cultural control (27, 28, 39, 61, 100, 103, 104, 121). The models typically identify an optimal control strategy for a fixed level of surveillance, for example, culling radii for removal of potentially infected citrus plants around an infected host (**Figure 3**). The models are used to identify how optimal control strategies change as the probability of detection changes, for example, using detection methods with different sensitivities (**Figure 3*a***). The models can also be used to infer the effects of different inherent cryptic periods on optimal culling radii (**Figure 3*b***) and hence on the impact and cost of control programs. Future work will address the question of how to optimize the allocation of resources for detection versus control when there is a fixed budget for dealing with an epidemic. Preliminary exploratory work has shown how to optimize the balance of expenditure on detection and control by applying optimal control theory to deterministic metapopulation models for disease management of sudden oak death (96).

Modeling surveillance and control programs simultaneously allows us to not only address the question of how much resource should be allocated to detection versus control (14, 35, 42, 91, 96) but also enable exploration of how, when, and where surveillance efforts should be targeted for optimal control. The analysis and use of spatial spread models for various invasive species indicate that surveillance should be targeted at locations in a landscape with higher probabilities of disease occurrence. The result is unsurprising, but identification of the preferred sites is not trivial. Epanchin-Niell et al. (36) developed a framework to optimize surveillance for the eradication of an invasive species. While testing the framework for gypsy moth in California (**Figure 4**), the authors showed that accounting for spatially varying surveillance costs and establishment risk could reduce annual management costs by 50% (36). By contrast, Berec et al. (10) compared a grid-based method with a random-sample method for invading insect pests and found that the spatial arrangement

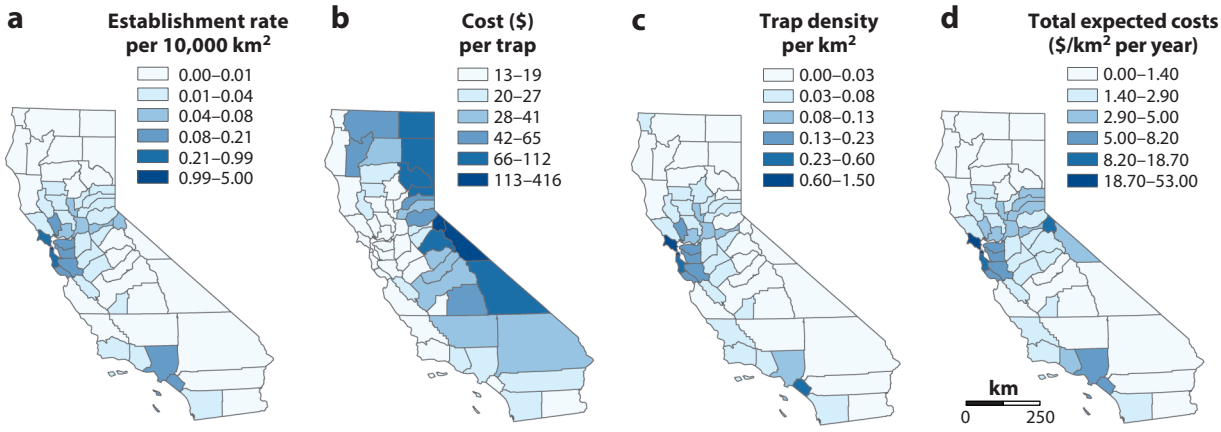

Figure 4

The use of models to inform optimal allocation of surveillance and control resources; the management of the gypsy moth in California (36). Shown is the parameterization of the model for different counties in California for (*a*) moth establishment rate (populations/10,000 km^2/year), (*b*) cost of trapping ($/trap), (*c*) optimal trap density (traps/km^2), and (*d*) the total expected costs of surveillance, eradication, and damages over time ($/km^2/year). (*a*,*b*) Sampling costs and establishment rates are heterogeneous across the region, which leads to a (*c*) spatially optimal deployment of traps, (*d*) reducing management costs by half compared with the actual trapping densities used. Adapted from Reference 36.

of traps was important in minimizing management costs only when trap sensitivity was high and budgets were low. Prioritizing site selection depends more broadly on the interaction of factors such as travel and other logistical costs (12), the sensitivity of detection, and the epidemiological characteristics of the host-pathogen system. Models, provided they do not become overly complex, can help in integrating these components to allow comparisons of different surveillance scenarios. The integration of passive, i.e., ad hoc, surveillance by growers, land managers, or members of the public with formal surveillance schemes also needs to be considered. Cacho et al. (19) found that eradication costs for an invasive species were greatly reduced when the additional survey effort provided by passive detections were included (19). This is an important area of further research for plant health, given recent developments in public engagement and citizen science initiatives (15, 25, 32, 34, 82, 89, 108). For plant diseases, more work is needed to explore how the control option at hand influences the optimal targeting of surveillance. For example, consider a control policy in which large numbers of hosts neighboring a single detected individual are removed, exemplified by the current *Xylella fastidiosa* 100-m radius policy in Europe (84) and the Asiatic citrus canker 1,900-ft removal policy in the United States (48). Detection of only one host plant is required to trigger removal of all surrounding hosts. Greater efficiency could be achieved, therefore, by targeting surveillance to discover new foci rather than wasting resources in taking multiple samples around known foci that would be removed in any event. Future work is likely to develop the integration of predictive models to improve the cost-effectiveness and efficiency of surveillance for emerging diseases.

CONCLUDING REMARKS

As the numbers of emerging pathogens and strains rise so does the importance of effective surveillance for control of emerging epidemics. In this review, we have explored how epidemiological information on disease dynamics can be used to inform and target surveillance strategies. Simple

Sample sensitivity: the probability that a sample will indicate a pathogen when the pathogen is present

but powerful statistical models of surveillance can be linked with epidemiological models to yield new insight into how surveillance should be matched to the characteristics of an epidemic. Statistical models can provide rules of thumb to enable us to answer questions such as: Following the first discovery of an epidemic, what incidence has it reached in the population? A range of spatial mapping approaches is available to capture spatial information on disease risk and allow improved targeting of surveys. Spatially explicit stochastic models enable disease dynamics to be fully captured and thus predict when, where, and how fast disease is most likely to spread across complex heterogeneous landscapes. This approach enables simulation of surveillance and control strategies to identify the optimal use of resources. In general, surveillance in agricultural landscapes and natural environments can be enhanced by increasing the intensity and coverage of surveys (i.e., the number and location of sites that are sampled) and by increasing our ability to detect disease when it is present at a particular location or plant (i.e., improved sample sensitivity). Limited fiscal budgets place restrictions on our ability to increase the former through traditional surveys and inspections. Consequently, a range of new forms of surveillance has been proposed, including the use of remote sensing (86), citizen science initiatives (15, 32, 82, 89), reports from growers (31), and diagnostic networks (93). However, it is still not clear what these new forms of detection tell us about epidemic dynamics and how they can be best utilized. For example, if a citizen scientist detects the first case of disease in a new area, how far will the disease have already spread by then? Also, do citizen scientists provide sufficient intensity of surveillance, and how should this be augmented with traditional surveys? Meanwhile, advances in detection and diagnostic technologies continue to improve sample sensitivity and provide ever more accurate, fast, and mobile diagnostic tools for plant health (31, 67, 85, 86).

Future work will determine how best to deploy these technologies effectively in complex and heterogeneous disease landscapes to detect and control emerging epidemics. There is also scope for comparative work to investigate the complementary advantages of using statistical and stochastic spatially explicit models to inform surveillance.

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