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Short communication

Management of invading pathogens should be informed by epidemiology rather than administrative boundaries

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ABSTRACT

Plant and animal disease outbreaks have significant ecological and economic impacts. The spatial extent of control is often informed solely by administrative geography – for example, quarantine of an entire county or state once an invading disease is detected – with little regard for pathogen epidemiology. We present a stochastic model for the spread of a plant pathogen that couples spread in the natural environment and transmission via the nursery trade, and use it to illustrate that control deployed according to administrative boundaries is almost always sub-optimal. We use sudden oak death (caused by *Phytophthora ramorum*) in mixed forests in California as motivation for our study, since the decision as to whether or not to deploy plant trade quarantine is currently undertaken on a county-by-county basis for that system. However, our key conclusion is applicable more generally: basing management of any disease entirely upon administrative borders does not balance the cost of control with the possible economic and ecological costs of further spread in the optimal fashion.

1. Introduction

The significant environmental damages and economic costs associated with invading plant and animal pathogens emphasize the importance of effective management (Pimentel et al., 2005). Epidemiological theory demonstrates how efficient control of disease requires matching the temporal and spatial scales of treatments with those of epidemics (Gilligan, 2008; Cunniffe et al., 2015a). Recent work also shows how epidemiological models can be linked to economics to balance the benefits of control against its costs (Ndeffo Mbah and Gilligan, 2010; Cunniffe et al., 2014). However, in practice, management of invading pathogens is often dominated by the geography of administrative or political boundaries. Plant trade quarantines are a notable example. For numerous plant pests and pathogens, including the emerald ash borer (Poland and McCullough, 2006), citrus greening (Stokstad, 2012) and the pine shoot beetle (Haack and Poland, 2001), initial detection triggers legislation leading to quarantine that is then applied uniformly across an entire administrative region, such as a county or state. However, pests and pathogens do not respect administrative boundaries. Therefore, control informed solely by these borders is likely to be sub-optimal.

We illustrate the general principle using the oomycete plant pathogen, *Phytophthora ramorum*, in California as a motivating example. Sudden oak death, caused by *P. ramorum*, has killed millions of oak and tanoak across coastal California. A large number of tree and shrub species are susceptible, including many species traded by nurseries (Rizzo et al., 2005). Outbreaks in the wider environment can therefore infect nursery plants, posing risks of subsequent long-range transmission via trade (Liebhold et al., 2012). If *P. ramorum* infection is confirmed within a Californian county, legislation mandates that all nurseries across that entire county must be quarantined (APHIS, 2012). Quarantine was extended to include Trinity County in April 2015 (Fig. 1a), after the pathogen was confirmed in the county near the Humboldt County border.

As proof of concept, in the following analysis we use mathematical modeling to illustrate principles underlying an epidemiologically-informed control strategy that is potentially more cost-effective (Fig. 1b). We consider a model for an invading plant pathogen that tracks the density of susceptible and infected hosts as an initially uninfected county becomes infected. After a delay to allow first detection of the pathogen in the county, we consider the effects of applying quarantine to the plant trade in part of the county, centered on the detected outbreak. We use the model

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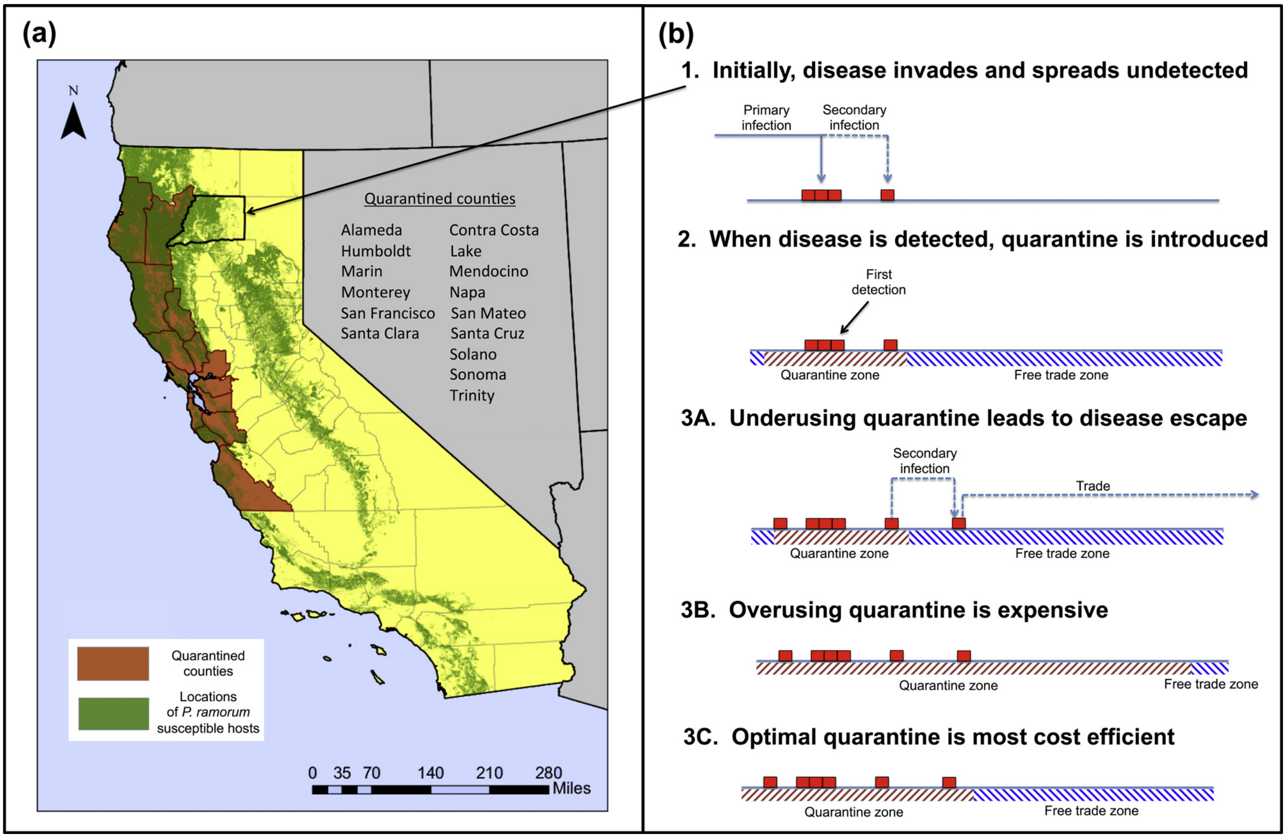

Fig. 1. (a) Location of *P. ramorum* hosts (Meentemeyer et al., 2011) and current quarantine counties in California; (b) a schematic showing how partial quarantine could be deployed if the pathogen appears in a new county. This indicates the consequences of sub-optimal and super-optimal sizes of the quarantine region.

to show that quarantine extending to the borders with the neighboring counties – but not beyond – is almost always sub-optimal.

2. Methods

2.1. Mathematical model

Primary infection and subsequent secondary spread of a plant pathogen are modeled in a county represented by a one-dimensional landscape. The county is initially uninfected. We use a stochastic Susceptible-Infected model (Keeling and Rohani, 2008), splitting the county of length W into $M+1$ equally sized patches (Fig. 2; Table S1). To allow for local bulk-up of the pathogen within each patch, we model each patch as containing a number of "host units", corresponding to vegetation susceptible to infection. We assume that a small proportion ρ of hosts are in nurseries, and $1-\rho$ are in the wider environment. The number of host units in patch i is $N_i = S_i + I_i$, which, for each simulation, we draw from a uniform distribution (Table S1).

Motivated in the context of sudden oak death by any of the number of inland Californian counties that contain hosts susceptible to *P. ramorum* (Fig. 1), we assume that there is an inoculum source outside the county corresponding to the ongoing epidemic in the coastal region of California. After first arrival in the county, the pathogen spreads within the county via secondary infection, and there can also be additional primary infection. Since the pathogen might arrive in the county via primary infection close by, followed by secondary infection into the county, we also include L patches on either side of the county in our model. This is how we define our host landscape: namely, the county plus small regions on either side of the county that lie in neighboring counties.

We account for two types of spread (Grünwald et al., 2012), using a mixture of two Cauchy dispersal kernels with a short-range and a long-range component, as used in the more detailed model of *P. ramorum* by Meentemeyer et al. (2011). Secondary infection of each susceptible host unit in patch j by each infected host unit in patch i therefore occurs at average rate $\beta\varphi_{ij}$, where β is the rate of infection, and where

$$\varphi_{ij} = \frac{\gamma}{N_{\max}} \int_{x_1}^{x_2} \frac{\left(1+(x/\alpha_1)^2\right)^{-1}}{F_1}\,\mathrm{d}x + \frac{1-\gamma}{N_{\max}} \int_{x_1}^{x_2} \frac{\left(1+(x/\alpha_2)^2\right)^{-1}}{F_2}\,\mathrm{d}x.$$

The integrals are over the width of patch j, so that x_1 is the distance between the center of patch i and the nearest edge of patch j, and x_2 is the distance between the center of patch i and the farthest edge of patch j. The parameter F_1 is a normalizing constant so that the dispersal kernel is a valid probability distribution,

$$\int_{-\infty}^{\infty} \frac{\left(1+(x/\alpha_1)^2\right)^{-1}}{F_1}\,\mathrm{d}x = 1.$$

with a similar expression for F_2. The factor of $1/N_{\max}$ is the probability that a unit of inoculum lands on the particular susceptible host unit when landing in patch j.

Primary infection from outside the county is assumed to occur according to the same dispersal kernel as within-county spread, but assuming that there is a source of infection corresponding to Z infected host units a distance d to the west of the county. For simplicity we assume the inoculum source corresponding to this distant epidemic is of a constant size. Consequently, primary