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Modelling the Impact and Control of an Infectious Disease in a Plant Nursery with Infected Plant Material Inputs

Andrew M. Bate^{a,*}, Glyn Jones^b, Adam Kleczkowski^c, Alan MacLeod^d, Rebecca Naylor^e, Jon Timmis^e, Julia Touza^a, Piran C. L. White^a

^a*Environment Department, University of York, Heslington, York. UK*

^b*The Food and Environment Research Agency (FERA), Sand Hutton, York. UK*

^c*Department of Computing Science and Mathematics, University of Stirling, Stirling. UK*

^d*Department for Environment, Food and Rural Affairs (DEFRA), Sand Hutton, York. UK*

^e*Department of Electronics, University of York, Heslington, York. UK*

Abstract

The ornamental plant trade has been identified as a key introduction pathway for plant pathogens. Establishing effective biosecurity measures to reduce the risk of plant pathogen outbreaks in the live plant trade is therefore important. Management of invasive pathogens has been identified as a weakest link public good, and thus is reliant on the actions of individual private agents. This paper therefore provides an analysis of the impact of the private agents' biosecurity decisions on pathogen prevention and control within the plant trade. We model the impact that an infectious disease has on a plant nursery under a constant pressure of potentially infected input plant materials, like seeds and saplings, where the spread of the disease reduces the value of mature plants. We explore six scenarios to understand the influence of three key bioeconomic parameters; the disease's basic reproductive number, the loss in value of a mature plant from acquiring an infection and the cost-effectiveness of restriction. The results characterise the disease dynamics within the nursery and explore the trade-offs and synergies between the optimal level of efforts on restriction strategies (actions to prevent buying infected inputs), and on removal of infected plants in the nursery. For diseases that can be easily controlled, restriction and removal are substitutable strategies. In contrast, for highly infectious diseases, restriction and removal are often found to be complementary, provided that restriction is cost-effective and the optimal level of removal is non-zero.

Keywords: bioeconomic model, plant disease, optimal control, plant nursery model

*Corresponding author: andrew.bate@york.ac.uk

1 **1. Introduction**

2 Increases in the movement of people and traded goods as a consequence of
3 globalisation have led to growing concerns about the threat posed by invasive species.
4 especially invasive pathogens of humans, plants and animals [e.g. 1–5]. Recent disease
5 outbreaks in plants, such as the Chalara fungus (*Hymenoscyphus pseudoalbidus*)
6 affecting ash trees across Europe [6] and the oomycete *Phytophthora ramorum*
7 affecting many plants including larch in Europe [7] and oaks in the US [8], have
8 focused attention on the policy options to reduce the risks of similar plant disease
9 outbreaks occurring in the future, and the management options to reduce damage
10 from newly established pathogen populations. These disease outbreaks have also
11 raised concerns about patterns of plant trade, which has been identified as a key
12 introduction pathway for invasive pathogens [9], and on the need for a more prominent
13 role of the private sector in biosecurity practices to mitigate existing risk [10].

14 Understanding the economic impacts of damage and mitigation is essential for
15 determining optimal policy and management options for invasive pathogens [11].

16 The body of the literature that combines invasion ecology with economic analysis
17 to deal with these issues has drastically increased in the last decade (for an overview
18 see [12, 13]). Bioeconomic studies explore the management problem from a central
19 authority perspective, focusing on the potential social welfare benefits from policy
20 intervention to limit the risk of invasive species damages using instruments that
21 include port inspections, quarantine and import tariffs [14, 15], import risk screening
22 programs [16, 17], the use of public funds to detect, eradicate and/or control
23 established invaders, and habitat restoration [e.g. 18–20]. Other studies have
24 examined the trade-off between preventive measures before the arrival and control
25 measures after the invader is known to be in the country in order to determine the
26 optimal allocation of limited public resources between these two strategies [e.g.
27 21–26] Here we add to this literature by adopting a private sector perspective, in order
28 to understand the biosecurity vulnerability and management incentives affecting
29 individual businesses.

30 One of the challenges for developing policy to reduce the risk of outbreaks of

31 pathogens is the fact that the potential routes of invasion are not only diverse, but
32 also that they are controlled by a mixture of public and private agents. Trading
33 decisions made by private decision-makers may have significant implications for public
34 interest at a regional or national level, but the public costs of an outbreak are likely to
35 far exceed the costs experienced by any one private business, and a privately optimal
36 trading decision is very unlikely to match the publicly optimal one due to potential
37 conflicting interests [27, 28]. Effective control of the risk posed by invasive pest and
38 diseases has been defined as a ‘weakest-link’ public good [e.g. 29, 30]. Therefore, the
39 risk of outbreak can be in the hands of a single private firm in the trading network.
40 This can limit the level of success of decentralised biosecurity efforts, although it may
41 also allow the firm to take a leadership role, creating incentives for other firms to take
42 action [31].

43 This paper studies the relationship between prevention and control strategies in the
44 context of plant trade. We take a single nursery perspective in order to understand
45 the biosecurity vulnerability and incentives affecting private firms, that can inform
46 subsequent analysis on networks and policy development . We develop a simple
47 bioeconomic model of a private nursery owner who buys in, grows and sells on plants
48 in the face of the threats posed by an infectious pathogen. The management options
49 available to the nursery owner are some combination of (1) restriction, i.e. prevention
50 measures to reduce the number of infected plant materials coming from input sources
51 (for example, inspecting inputs and/or investigating and discriminating input suppliers
52 based on perceived cleanliness) and (2) removal, i.e. taking out infected plants within
53 the nursery. Other means of management like cleanliness and fungicide use are
54 assumed to at constant optimal levels.

55 Prior bioeconomic research on the plant trade has focused on its role as a
56 significant pathway to the introduction of potentially exotic invasive plants, exploring
57 the use of taxes or annual license fee to reduce this risk and cover the expected
58 environmental damages [32, 33]. However, implementing these market-based
59 instruments is challenging due to the lack of support among stakeholders in the
60 industry [34, 35]. In this paper, we follow current research on private biosecurity
61 responses to livestock diseases, where disease risk does not only depend on agents’
62 choices but also is characterized by an underlying epidemiological dynamics [36]. In

63 this framework, [37] are concerned on the management problem characterized by
64 livestock-wildlife interactions in disease transmission; and [38] studied the role of
65 government policies as regular testing on encouraging farmers' biosecurity investments.
66 More recently, [39] focused on assessing whether trade always increase risk or whether
67 it can act as a disease management mechanism.

68 Our focus, however, is the threat associated with private trading decisions, as
69 infected goods can be bought in and sold on. We contribute to the above work by
70 focusing on plant trade, and addressing the role of both private preventing and
71 controlling behaviour to limit disease transmission risk characterized by
72 epidemiological dynamics. Thus, we examine the potential trade-offs and synergies
73 between these management decisions when the nursery owner's objective is to minimize
74 the expected private costs from infection management and revenue losses associated
75 with the reduced value of infected plants. We find that if the disease spreads faster
76 than the ability to control the disease, removal and restriction complement each other
77 whereas if the disease is controllable, removal and restriction become substitutes.

78 **2. Model derivation**

79 *2.1. Disease dynamics*

80 We consider a plant nursery with a nursery owner who constantly buys plant
81 material, grows it and sells it on when the plant becomes mature (i.e. reaches a target
82 age). A disease is introduced within the input plant material and spreads within the
83 nursery. For simplicity and generality, we assume that the plant population is split
84 into two classes, susceptible plants (S) and infected plants (I). Infected plants can
85 infect susceptible plants, and once infected a plant remains infected for the rest of its
86 time in the nursery; there is no recovery from the infection¹. The consequence of
87 infection for the nursery owner is that infection alters (assumed here to reduce) the
88 net price obtained from selling of a mature plant.

89 To combat the spread of the infection within the nursery, the nursery owner has
90 two different control measures. The owner can invest (i) in **restriction** to reduce the

¹Although there is no recovery, infected plants can leave the system via being sold on or being removed and be replaced by a susceptible plant. This means there is some kind of pseudo-recovery, meaning the system behaves more like a classic SIS system than SI.

91 proportion of infected inputs (be it from inspecting inputs and rejecting infected
 92 plants or by selecting suppliers with less infected material); and (ii) in the **removal** of
 93 infected plants within the nursery. Removal reduces the time an infected plant stays in
 94 the nursery, avoiding additional secondary invasions, but provides no revenue.

Schematically, the plant-disease dynamics can be described as (see Fig 1):

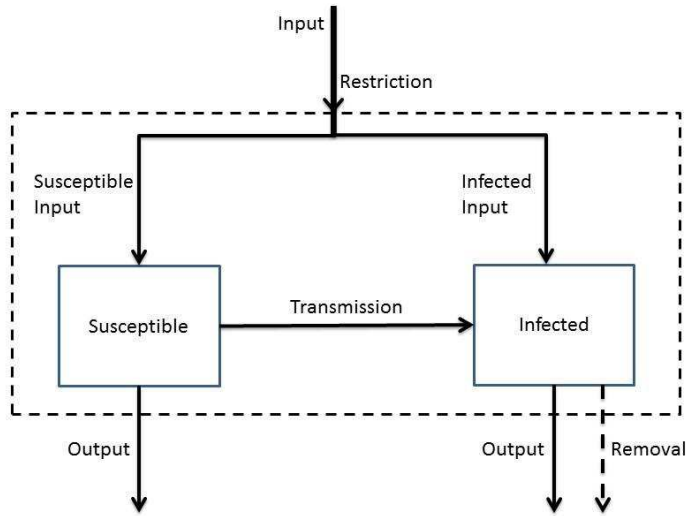


Figure 1. A transfer diagram representing the disease dynamics within the nursery

95

96 Change in S = Input of S - Output of S - Disease Transmission,

97

98 Change in I = Input of I - Output of I - Removal of I + Disease Transmission.

99

100 For simplicity, we assume that the stock of plants at the nursery is fixed, N , which
 101 may mean for example that the nursery is always full (this is a simplifying assumption
 102 that is not necessarily realistic; we address this in the Discussion). To do this, we set
 103 Total Input=Total Output + Removal, where Output of $S = \delta S$ and Output of $I = \delta I$,
 104 where δ is the rate of plants become mature and sold off (i.e. plants stay for an
 105 expected time of δ^{-1} in the absence of removal)². This means instantaneous
 106 replacement of any removed plant is assumed; when something is either sold or
 removed by control, it is immediately replaced to keep the stock at nursery constant.

106

²Another approach is to have assume that infected plants stay longer in the nursery due to slower growth. However, this approach would ultimately lead to the same reduction in revenue, since revenue is price \times output. Consequently, the only real difference would be that different output rates would lead to a more complex replacement term.

107 $I = u_{rem}I$, where u_{rem} is removal control effort (with units of removal effort per
 108 infected plant per unit time). We will assume that u_{rem} is bounded between 0 and
 109 u_{remmax} , the maximum possible effort spent on removal. Incorporating this, we have:

$$\text{Total Input} = \delta(S + I) + u_{rem}I. \quad (1)$$

110 This input is split between susceptible and infected plants; $p(u_{ins})$ is the proportion of
 111 plant inputs that are infected (as a function of restriction effort per unit time u_{ins} ,
 112 which is a control variable) and thus $(1 - p(u_{ins}))$ is the proportion of plant inputs
 113 that are susceptible.

Incorporating the control measures into standard SI equations [40–42], and
 assuming density dependent transmission (βSI), we get:

$$\frac{dS}{dt} = (1 - p(u_{ins}))(\delta(S + I) + u_{rem}I) - \delta S - \beta SI, \quad (2)$$

$$\frac{dI}{dt} = p(u_{ins})(\delta(S + I) + u_{rem}I) - \delta I - u_{rem}I + \beta SI. \quad (3)$$

114 Given the assumption of constant total plant stock at the nursery ($S + I = N$), we
 115 can reduce the system down to one equation by substitution $S = N - I$. We can also
 116 rescale the infected population by the total population and consider disease prevalence,
 117 $i = \frac{I}{N}$, the proportion of infected plants in the population ($0 \leq i \leq 1$).

118 Then we get:

$$\frac{di}{dt} = \frac{1}{N} \frac{dI}{dt} = p(u_{ins})(\delta + u_{rem}i) - \delta i - u_{rem}i + \beta N(1 - i)i. \quad (4)$$

119 Furthermore, we rescale time by δ^{-1} , the expected time a susceptible plant stays in
 120 the nursery. Consequently, $\tau (= \delta t)$ is the number of generations. Thus:

$$\frac{di}{d\tau} = p(u_{ins})(1 + \hat{u}_{rem}i) - i - \hat{u}_{rem}i + R_0(1 - i)i, \quad (5)$$

121 where $\hat{u}_{rem} = u_{rem}\delta^{-1}$, the removal effort per plant generation (which is bounded
 122 above by $\hat{u}_{remmax} = u_{remmax}\delta^{-1}$), and $R_0 = \beta N\delta^{-1}$, the basic reproductive number,
 123 the expected number of secondary infections from a single infected plant over the
 124 lifespan of the infected plant in the nursery in an otherwise wholly susceptible plant

125 stock. The basic reproductive number is fundamental to whether a disease will spread
126 and is discussed in the results section.

127 As mentioned previously, the proportion of plants brought into the nursery being
128 infected ($p(u_{ins})$) is a function of restriction (u_{ins}). We assume that the proportion of
129 infected plant inputs has the following properties:

- 130 • $p(u_{ins})$ is a continuously differentiable function of the restriction effort u_{ins} .
- 131 • With no restriction of plant inputs ($u_{ins} = 0$), some proportion of infected
132 plants, a , will enter the nursery, i.e. $p(0) = a$ where $a \in (0, 1]$.
- 133 • With any finite restriction effort, some proportion of infected plant will enter the
134 nursery, i.e. $p(u_{ins}) > 0$ for all finite u_{ins} . This means that it is not possible to
135 completely stop infected inputs from arriving no matter how high the level of
136 effort, be it from the difficulty to recognise asymptomatic infected inputs, or
137 machine and human error.
- 138 • For all restriction effort, increasing restriction effort reduces the proportion of
139 infected plant entering the nursery, i.e. $p(u_{ins})$ is a monotonically decreasing
140 function of u_{ins} (equivalently, $\frac{dp}{du_{ins}} \leq 0$ everywhere).

141 Any function that is (a) continuous, (b) bounded below (by zero in this case) and (c)
142 monotonically decreasing, must converge to some limit as u_{ins} goes to infinity. We
143 denote this limit b , the proportion of inputs that are infected when unlimited
144 restriction effort is used, where $b \in [0, a]$. A simple candidate that satisfies all of these
145 characteristics is $p(u_{ins}) = (a - b) \exp(-du_{ins}) + b$, is plotted in Fig 2 for various
146 values of d , where d can be interpreted as the effort-effectiveness of the restriction
147 measures, i.e. the reduction in the proportion of infected plant inputs per unit of
148 restriction effort.

149 2.2. Bioeconomic model

150 We consider a price-taking representative nursery owner who seeks to maximise
151 profit, faced with the impact of an infectious plant disease. In our model, two types of
152 outputs are taken into account: fully matured susceptible and infected plants with P_S

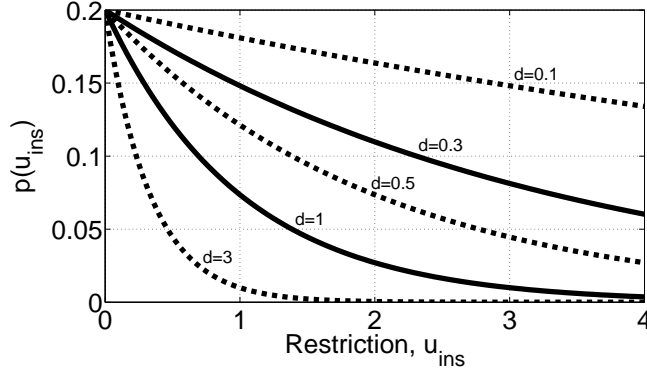


Figure 2. Proportion of infected plant inputs, $p(u_{\text{ins}})$, where $p(u_{\text{ins}}) = (a - b)\exp(-du_{\text{ins}}) + b$ with $a = 0.2$, $b = 0$ and various of values of d
The solid lines are values used in Scenarios found in the Results.

153 and P_I representing the unit net price of those outputs, respectively³. We assume that
 154 $P_I < P_S$ since the infection would likely decrease the plants value when mature and
 155 could incur higher production costs⁴. The dynamics of the proportion of infected
 156 plants within the nursery is given by equation (5). In addition, we assume that disease
 157 symptoms become more apparent as infected plants mature. This, together with an
 158 assumption of a regime of inspections within the nursery (inspection regime is
 159 independent of the state of the nursery, i.e. a constant cost and thus can be ignored),
 160 leads to the nursery owner having good knowledge of which plants are infected and so
 161 can act accordingly if desired. All the mature plants sold, or those subject to removal
 162 control, are immediately replaced given a constant price P_{in} of plant inputs. This is
 163 consistent with our earlier assumption of constant stock within the nursery.

164 We also consider the costs of removing infected plants and undertaking restrictions
 165 measures to prevent buying infected input plant material. The cost of removing
 166 infected plants should increase both with the number of infected plants and with the
 167 removing control effort, u_{rem} . Consequently, we will assume for simplicity that the
 168 cost of removing infected plant is linearly dependent on the number of infected plants
 169 and to prevent the unfeasible case of unbounded removal control effort, we will set a
 170 maximal value of removal control effort of u_{remmax} . Similarly, the cost of the

³We assume a fixed price for plant outputs and inputs for simplicity. However, it has been suggested that nurseries work under monopolistic competition[33].

⁴A few diseases can be beneficial, e.g. mild infestations of *Botrytis cinerea* on grapes results in noble rot, which is desirable for dessert wines; in such cases where $P_I > P_S$, the optimal control is always to do nothing, which is trivial.

171 restriction regime is proportional to the restriction effort u_{ins} , assumed to be
 172 dominated by fixed costs and thus is independent from the level of removal effort and
 173 number of infected plants (i.e. there is no additional cost from restricting measures
 174 when buying input material to replace the removed infected plants).

175 The management decision problem is to maximise the present value profits by
 176 selecting the level of control in restriction and removal measures over the time horizon
 177 T and is characterised by the optimising equation:

$$\max_{u_{ins}, u_{rem}} \text{Profit} = \int_0^T \underbrace{e^{-rt}}_{\text{Discounting}} \left(\underbrace{P_S \delta S}_{\text{Revenue from selling S}} + \underbrace{P_I \delta I}_{\text{Revenue from selling I}} \right. \quad (6)$$

$$\left. - \underbrace{P_{in}(\delta N + u_{rem} I)}_{\text{Purchase of replacement stock}} - \underbrace{c_{rem} u_{rem} I}_{\text{Cost of removing}} - \underbrace{c_{ins} u_{ins}}_{\text{Cost of restriction}} \right) dt$$

178
 179 subject to Equations (2) and (3) where $u_{rem} \in [0, u_{remmax}]$ and $u_{ins} \geq 0$, and where r
 180 is the discount rate. Equation (6) is very amenable to analytic techniques around
 181 static solutions if we focus on the terms within the brackets. This means ignoring the
 182 discounting terms and the effects around terminal and initial conditions by assuming
 183 the terminal time is large enough for dynamics solution to have converged to the static
 184 solution. These static solutions will be the focus of this paper. Appendix C
 185 demonstrates that taking the Hamiltonian approach with optimal conditions used in
 186 much of the economic literature (using Pontryagin's maximum principle [43]) and then
 187 assume constant controls, will arrive at the same optimality conditions, perturbed by a
 188 term proportional to the discount rate (which is rescaled to $\hat{r} = \frac{r}{\delta}$). This discounting
 189 perturbation should be negligibly small since plant nurseries usually keep plants for a
 190 few months, possibly up to a couple of years.

191 Taking the static problem, and rescaling parameters and variables in (6) as for (5),
 192 we get:

$$\max_{\hat{u}_{ins}, \hat{u}_{rem}} P_S(1 - i) + P_I i - P_{in}(1 + \hat{u}_{rem} i) - c_{rem} \hat{u}_{rem} i - \hat{u}_{ins} \quad (7)$$

193 subject to Equation (5) where $\hat{u}_{rem} = u_{rem}\delta^{-1} \in [0, \hat{u}_{remmax}]$ (as before),

194 $\hat{u}_{remmax} = u_{remmax}\delta^{-1}$ and $\hat{u}_{ins} = c_{ins}u_{ins}(\delta N)^{-1}$.

195 Note that u_{ins} has been rescaled to \hat{u}_{ins} , which now represents restriction control
 196 costs (with units of restriction cost per plant in nursery per unit time). Thus, we need
 197 to define the proportion of infected inputs as a function of this rescaled restriction
 198 control cost. For the case $p(u_{ins}) = (a - b)\exp(-du_{ins}) + b$, as
 199 $\hat{p}(\hat{u}_{ins}) = (a - b)\exp(-\hat{d}\hat{u}_{ins}) + b$ where $\hat{d} = d\delta N c_{ins}^{-1}$ such that $\hat{p}(\hat{u}_{ins}) = p(u_{ins})$. Here
 200 \hat{d} represents the cost-effectiveness of restriction efforts, i.e. the reduction in the
 201 proportion of infected inputs per dollar invested in restricting measures.

202 Given some terms are constant and thus have no influence on the optimised
 203 solution, we can simplify slightly and gather terms in the objective function (7) to
 204 arrive at

$$\max_{\hat{u}_{ins}, \hat{u}_{rem}} \left(\underbrace{\text{revenue lost from infected}}_{P_I - P_S} - \underbrace{\text{costs of removing and replacing infected}}_{(P_{in} + c_{rem})\hat{u}_{rem}} \right) i - \underbrace{\text{restriction costs}}_{\hat{u}_{ins}}. \quad (8)$$

205 Equation (8) can be simplified further by setting $L := P_S - P_I$ and
 206 $C := P_{in} + c_{rem}$. Therefore, L is the loss incurred from selling a mature infected plant
 207 instead of a mature susceptible plant, whereas C is the total cost of removing which
 208 includes both the expenses associated with the removal and replacement of an infected
 209 plant. Using this notation, it becomes clear that the nursery owner management
 210 problem consists of minimising the loss in revenue due to selling infected plants and
 211 the costs of management (removal and restriction). To simplify notation further, we
 212 will henceforth remove all the hats (i.e. set \hat{u}_{rem} as u_{rem} , \hat{u}_{ins} as u_{ins} , $\hat{p}(\hat{u}_{ins})$ as
 213 $p(u_{ins})$ and \hat{d} as d).

214 Consequently, the nursery management decision is to choose between the two
 215 control strategies to minimise these costs of the infection,

$$\min_{u_{ins}, u_{rem}} Q := (L + Cu_{rem})i + u_{ins} \quad (9)$$

216 subject to

$$\frac{di}{d\tau} = p(u_{ins})(1 + u_{rem}i) - i - u_{rem}i + R_0(1 - i)i, \quad (10)$$

217 where $u_{ins} \geq 0$ and $u_{rem} \in [0, u_{remmax}]$.

218 2.3. Analysis

219 We start the analysis of the system (9)-(10) by looking at the long term disease
220 dynamics for a given constant control regime. We compare the case where restriction
221 is perfect, i.e. all plant inputs are susceptible ($p(u_{ins}) = 0$) with a case where
222 restriction is imperfect, i.e. some plant inputs are infected ($p(u_{ins}) > 0$). Following
223 this, we derive the necessary conditions describing optimal level of effort in restriction
224 and removal strategies, using the equilibrium found in the imperfect restriction section.
225 Subsequently, we demonstrate some of the theoretical results with numerical solutions.
226 For simplicity, we will focus on exploring how the optimal level of management
227 changes with respect to changes in key parameters: the basic reproductive number
228 (R_0), the loss in revenue from selling an infected mature plant (L) and the
229 cost-effectiveness (d) (the decay in the proportion of infected plant inputs per dollar
230 spent in restriction efforts) and keep all other parameters fixed. This means, as a
231 baseline, we assume that (i) the background level of infection within the input plant
232 material is $a = 0.2$, so the disease is widespread within the traded plant material; (ii)
233 it is possible to restrict all infected inputs with unlimited restriction $b = 0$, and (iii)
234 the cost of removing and replacing an infected is set at $C = 10$. The nursery's
235 maximum level of effort on removal is assumed to take any value up to $u_{remmax} = 6$.

236 For the basic reproductive number, we will consider two cases, $R_0 = 0.5$ (i.e. the
237 disease cannot spread within the nursery, Scenario 1) and $R_0 = 5$ (i.e. the disease
238 spreads fast within the nursery, Scenario 2). Although the value of R_0 will depend on
239 the characteristics of the particular disease and the plant, given that established
240 human diseases can have values up to the mid teens (measles has a value of
241 $R_0 = 12 - 18$) and that many human diseases have basic reproductive numbers in the
242 realms of 5 [41], values of R_0 have rarely been found in plants diseases. Even though,
243 one study has found that R_0 is of the order of 50 for wheat stripe rust in large wheat
244 fields [44]. Moreover, the values of R_0 is a factor that depends not only on disease
245 traits, but also on the properties of the nursery. For example, actions like the routine

246 application of fungicides, the routine cleaning of equipment or the arranging the
247 nursery to limit contact between plants could lower R_0 . Consequently, one could
248 consider Scenario 1 as the case where the nursery has effective cleanliness whereas
249 Scenario 2 is where there is a lack of effective cleanliness.

250 For the loss of revenue from selling an infected plant, we consider a value of $L = 10$
251 as our baseline, which implies that the costs of removal are the same as the losses made
252 from selling an infected plant; this would be compared to scenarios with smaller values
253 for L , in particular, in Scenario 1b, $L = 5$ and in Scenario 2b, $L = 1$. It is reasonable
254 to assume that smaller values of L would correspond to situations where the diseased
255 plants have superficial damage and/or there are secondary markets for infected plant
256 outputs with little difference in the net price of healthy mature plants. Higher values
257 of L correspond to diseases that have a large impact on the net price of a highly
258 valuable plant, without an effective secondary market for infected plants. In particular,
259 plants with that take a long time to mature or bespoke plants sold to the landscape
260 sector tend to sell for higher prices and thus prone to large losses from infection.

261 Lastly, for the cost-effectiveness parameter, we consider $d = 1$ as the baseline.
262 $d = 1$ corresponds with a $(1 - \exp^{-1}) \times 100\%$ ($\approx 63\%$) reduction in the proportion of
263 infected plants coming into the nursery ($p(u_{ins})$) with an additional unit in restriction
264 (solid red line in Fig 2). For comparison, we assume $d = 0.3$ for scenarios where the
265 disease is costly to restrict (Scenario 1c and 2c). Using $d = 0.3$ corresponds with a
266 $(1 - \exp^{-0.3}) \times 100\%$ ($\approx 26\%$) reduction in $p(u_{ins})$ when the restriction costs increase
267 by one unit (solid blue line in Fig 2). Traits of systems where d is large are where it is
268 easy to detect infected plant inputs, because either the inputs have symptoms that can
269 be spotted by eye or there exist diagnostic technology that is cheap, quick and easy to
270 use. On the other hand, traits of systems where d is small are measures that require a
271 lot of labour, time or machinery to detect infected plant inputs. We suspect that this
272 is often true for bacteria, viruses and such with no clear symptoms in infected inputs,
273 which need expensive and potentially time-consuming tests to detect infected inputs.

274 Putting this all together, we have six different cases, three of which are where the
275 disease is not particular infectious (which will collectively be known as Scenario 1) and
276 three of which consider a highly infectious disease (collectively known as Scenario 2).
277 A summary of all six Scenarios, including results, is in Table 1.

Table 1. The Scenarios and their key results.

Scenario	R_0	L	d	$\downarrow p$	Optimal result
1a	0.5	10	1	63%	Maximum removal with restriction
1b	0.5	5	1	63%	No removal with restriction
1c	0.5	10	0.3	26%	Maximum removal, no restriction
2a	5	10	1	63%	‘Do nothing’ if $u_{remmax} \lesssim 3.5$, else maximum removal with restriction
2b	5	1	1	63%	‘Do nothing’ is optimal everywhere
2c	5	10	0.3	26%	‘Do nothing’ if $u_{remmax} \lesssim 4.75$, else maximum removal with restriction

Here, ‘ $\downarrow p$ ’ is the reduction of infected inputs from an increase in costs of restriction in one unit (i.e. $(1 - \exp(-d)) \times 100\%$ rounded to the nearest percentage point). ‘Do nothing’ means zero removal and zero restriction.

278 3. Results

279 3.1. Long term disease dynamics

280 3.1.1. Perfect restriction ($p(u_{ins}) = 0$)

281 In the absence of the removal of infected plants (i.e. $u_{rem} = 0$), we have two cases:

282 (1) $R_0 < 1$: In this case, on average, a single infected plant infects less than one
 283 susceptible plant over the lifetime of the infected plant and hence the disease will die
 284 out eventually. Consequently, the only stable state is the disease-free state and thus
 285 the disease cannot become endemic ($i^* = 0$) (Fig 3(b)). (2) $R_0 > 1$: Here, a single
 286 infected plant infects more than one susceptible over the lifetime of the infection and
 287 hence the disease will spread out from any single introduction. Hence, the only stable
 288 steady state is the endemic steady state $i^* = 1 - \frac{1}{R_0}$ and thus any introduction will
 289 result in the disease being endemic (Fig 3(a)).

290 In the presence of the removal of infected plants (i.e. $u_{rem} > 0$), the results are
 291 similar to the absence of removal, except the threshold between a disease-free nursery
 292 and an endemic disease in the nursery is based on value of $R_0^{rem} = \frac{R_0}{1+u_{rem}}$. For
 293 $R_0^{rem} > 1$, for any introduction of disease, the disease will invade and approach the
 294 steady state $i^* = 1 - \frac{1}{R_0^{rem}}$ (Fig 3(a)). For $R_0^{rem} < 1$, the disease will not become
 295 endemic from any single introduction (Fig 3(b)).

296 Now, for $u_{rem} > 0$, we have that $R_0^{rem} < R_0$. Thus, the disease will find it harder
 297 to survive as infected plants have less time in the nursery to infect other plants

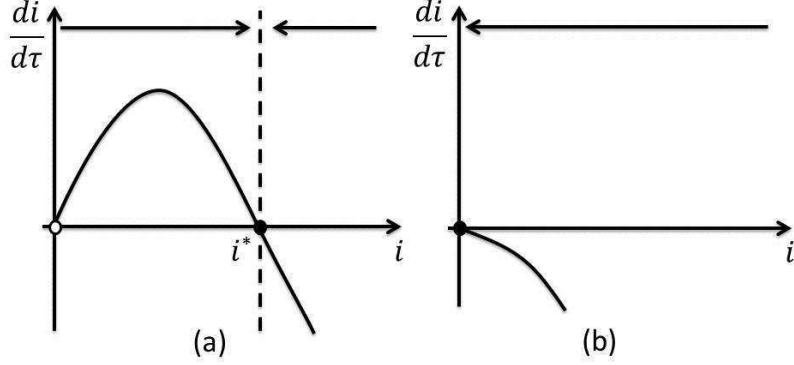


Figure 3. Perfect restriction ($p = 0$)

(a) If $R_0^{rem} = \frac{R_0}{1+u_{rem}} > 1$, then the prevalence equation is a form of Logistic growth. There are two steady states (where $\frac{di}{d\tau}$), $i^* = 0$ and $i^* = 1 - \frac{1}{R_0^{rem}}$. $i = 0$ is unstable and that for the region between $i = 0$ and $i = 1 - \frac{1}{R_0^{rem}}$, $\frac{di}{d\tau} > 0$ and thus disease prevalence will increase over time (represented by the arrow at the top). (b) If $R_0^{rem} < 1$, then the prevalence equation is negative for all positive prevalence. There is one non-negative steady state, $i^* = 0$, which is stable. Note that when $u_{rem} = 0$, $R_0^{rem} = R_0$.

298 because of removal. In particular, if the removal effort (u_{rem}) is sufficiently large
 299 ($u_{rem} > R_0 - 1$), we can reduce R_0^{rem} below 1 and consequently rid the nursery of the
 300 disease in the long run.

3.1.2. Imperfect restriction ($p(u_{ins}) = p > 0$)

302 With imperfect restriction, the disease will always persist in the nursery plant stock
 303 to some level (Figure 4). There is always only one steady state that is non-negative,

$$i^* = \frac{R_0 - 1 - (1-p)u_{rem} + \sqrt{(R_0 - 1 - (1-p)u_{rem})^2 + 4pR_0}}{2R_0}, \quad (11)$$

304 and it is always stable. The lack of a disease-free steady state is due to the constant
 305 inflow of infected plants into the system. In particular, $\frac{di}{d\tau} = p > 0$ at $i = 0$ and thus
 306 disease prevalence will always increase when starting with a disease-free nursery.

307 Despite the disease always persisting in the nursery, we wish to distinguish between
 308 two cases. If $R_0^p = \frac{R_0}{1+u_{rem}(1-p)} > 1$ (Fig 4(a)), the disease spreads through the plant
 309 stock like before. Notice that $R_0 > R_0^p > R_0^{rem}$. This is because the removal control is
 310 only effective $(1-p) \times 100\%$ of the time, since $p \times 100\%$ of the time in the removing
 311 infected is replaced by another infected. In particular, if $p = 0$, $R_0^p = R_0^{rem}$, whereas
 312 for $p = 1$, $R_0^p = R_0$. Consequently, imperfect restriction undermines the removal
 313 control. In particular, if $R_0^{rem} > 1$, the disease would persist without any infected

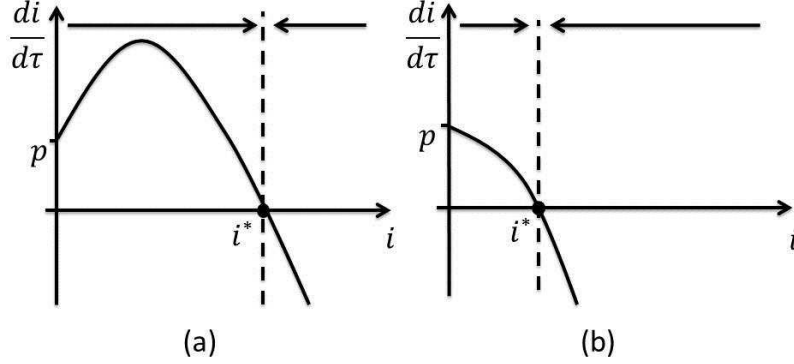


Figure 4. Imperfect restriction ($p > 0$)
 (a) $R_0^p = \frac{R_0}{1+u_{rem}(1-p)} > 1$ and (b) $R_0^p = \frac{R_0}{1+u_{rem}(1-p)} < 1$. For both figures have only one steady state that is stable; there is no disease-free steady state unlike the case with $p = 0$.

314 inputs (as shown in the previous subsection for perfect restriction). If $\frac{R_0}{1+u_{rem}(1-p)} < 1$
 315 (Fig 4(b)); the disease does not spread effectively within the nursery and instead its
 316 persistence in the nursery is dependent on constant introduction of infected plant
 317 inputs into the nursery.

318 The disease dynamics for the imperfect restriction are essentially logistic growth
 319 with an additional constant introduction of infected plants. In particular, Fig 4(a) can
 320 be seen as a shifted and transformed version of the logistic growth in Fig 3(a), which
 321 results in the loss of the disease-free steady state and an increase in the endemic
 322 steady state. Likewise, Fig 4(b) can be seen as a shifted version of the ‘negative
 323 logistic growth’ in Fig 3(b), where the disease-free steady state becomes an endemic
 324 steady state.

325 Table 2 summarises the results about when the disease is endemic in the nursery
 326 for both the perfect and imperfect restriction.

Table 2. Summary of Constant Control.

	Endemic	Disease-free
Perfect Restriction, no removal	$R_0 > 1$	$R_0 < 1$
Perfect Restriction with removal	$R_0^{rem} > 1$	$R_0^{rem} < 1$
Imperfect Restriction	Always	Never

Here, $R_0^{rem} = \frac{R_0}{1+u_{rem}}$.

327 3.2. Optimal management: Analytical results

328 Working with the prevalence steady state, we seek to find the optimal combination
 329 of removal and restriction, u_{rem} and u_{ins} that minimises the costs of the plant disease

330 at the nursery:

$$Q = (L + Cu_{rem})i^* + u_{ins} = (L + Cu_{rem})\frac{M + \sqrt{M^2 + 4R_0p(u_{ins})}}{2R_0} + u_{ins} \quad (12)$$

331 where $M(u_{ins}, u_{rem}) = R_0 - 1 - (1 - p(u_{ins}))u_{rem}$. Note, M is fundamentally linked
 332 with R_0^p with equivalent threshold properties: $M = 0$ corresponds with $R_0^p = 1$, $M > 0$
 333 corresponds with $R_0^p > 1$ and $M < 0$ corresponds with $R_0^p < 1$.

To find the combination of u_{rem} and u_{ins} that minimise Q , we need to consider the partial derivatives of Q to find internal and boundary minima. When optimal prevention and control policies are interior they satisfy the first order conditions:

$$\frac{\partial Q}{\partial u_{rem}} = MC_{rem} - MB_{rem} = 0 \quad (13)$$

$$\frac{\partial Q}{\partial u_{ins}} = MC_{ins} - MB_{ins} = 0 \quad (14)$$

where

$$MB_{rem} = \frac{(L + Cu_{rem})(1 - p(u_{ins}))}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0p(u_{ins})}} \right)$$

$$MC_{rem} = \frac{C}{2R_0} \left(M + \sqrt{M^2 + 4R_0p(u_{ins})} \right)$$

$$MB_{ins} = -\frac{(L + Cu_{rem})\frac{\partial p(u_{ins})}{\partial u_{ins}}}{2R_0} \left(u_{rem} + \frac{Mu_{rem} + 2R_0}{\sqrt{M^2 + 4R_0p(u_{ins})}} \right)$$

$$MC_{ins} = 1$$

334 As expected, Equation (13) (Equation (14)) requires a nursery owner to allocate
 335 resources to removal (restriction) until the last dollar spent on removal (restriction)
 336 equals the marginal benefits gained in terms of reduction in infection costs. The
 337 analysis of the properties of local and global minima for removal (Equation (13)) and
 338 restriction (Equation (14)), can be found in Appendices A and B, respectively.

339 Looking at Equations (13) and (14) and incorporating the results found in
 340 Appendices A and B, we have the following:

- 341 • With respect to removal, if $MB_{rem} > MC_{rem}$ at $u_{rem} = 0$ then $MB_{rem} > MC_{rem}$
 342 for all u_{rem} and thus $u_{rem} = u_{remmax}$ is the global minimum with respect to
 343 u_{rem} .

- 344 • If $MB_{rem} < MC_{rem}$ at $u_{rem} = u_{remmax}$ then $MB_{rem} < MC_{rem}$ for all admissible
345 u_{rem} and thus $u_{rem} = 0$, i.e. no removal effort, is the global minimum with
346 respect to u_{rem} .
- 347 • The only other case with respect to u_{rem} is that there exists a value of
348 $u_{rem} \in (0, u_{remmax})$ such that $MB_{rem} = MC_{rem}$, and this internal solution is a
349 local maximum. Both $u_{rem} = 0$ and $u_{rem} = u_{remmax}$ are local minima with
350 respect to u_{rem} . One of these will be the global minimum with respect to u_{rem}
351 and direct comparison of the values of Q at these local minima is required.
- 352 • With respect to restriction, if $MB_{ins} < MC_{ins}$ at $u_{ins} = 0$, then $MB_{ins} < MC_{ins}$
353 for all $u_{ins} > 0$ and thus Q is minimised at $u_{ins} = 0$, i.e. no restriction is optimal.
- 354 • Conversely, if $MB_{ins} > MC_{ins}$ for $u_{ins} = 0$ (for fixed u_{rem}), then there is a value
355 of $u_{ins} > 0$ such that $MB_{ins} = MC_{ins}$ (i.e. a level of restriction where the
356 marginal benefit is equal to the marginal cost), and this value is the global
357 minimum with respect to u_{ins} , i.e. moderate restriction is optimal.
- 358 • One can analyse whether removal and restriction work together as complements
359 or as substitutes by analysing $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}}$. For complements, $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} < 0$
360 (since Q represents costs, not profit or utility) and $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} > 0$ for substitutes.
361 The expression for $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}}$ is complex and can be either sign. In particular, if
362 M and R_0 are large and u_{rem} is zero, then $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} < 0$ and thus restriction
363 and removal are complements; whereas, if u_{rem} is large and thus M is large and
364 negative, $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} > 0$, making restriction and removal substitutes.

365 From this and by looking at Equations (13) and (14), we can establish some rules
366 of thumb. Firstly, by looking at Equation (14), we can see that increasing L and/or C ,
367 will increase the marginal benefits in damages avoided and thus generally results in
368 higher restriction (in particular, it never leads to lower levels of restriction). Secondly,
369 looking at Equation (13), we can see that increasing L and C proportionally results in
370 no change in whether $u_{rem} = 0$ or $u_{rem} = u_{remmax}$ are optimal. Consequently, the
371 values of L and C themselves have no impact on the optimal strategy for removal, only
372 the ratio between L and C (in other words, the nursery owner would apply the same
373 effort if losses for an infected plant were \$1 and removal costs \$1 as \$10 losses with \$10

374 removal costs, it is just a matter of scale). This is not the case for u_{ins} , since both,
 375 revenue losses and removal costs are compared with the cost of restriction.

376 The effects of R_0 and the parameters in $p(u_{ins})$ on Equations (13) and (14) are not
 377 straightforward, partly because they are also included within M , although the presence
 378 of $\frac{\partial p(u_{ins})}{\partial u_{ins}}$ in MB_{ins} suggests that increasing the cost-effectiveness of restriction, d ,
 379 increases MB_{ins} around $u_{ins} = 0$, making restriction measures more likely.

380 3.3. Optimal management: Numerical solutions

381 Table 1 provides a summary of the results for all the scenarios analysed.

382 3.3.1. Scenario 1: Low infectiousness

383 Scenario 1 represents cases of diseases that would not persist in the nursery
 384 without the constant introduction of infected plant materials. First we will consider
 385 the baseline case where $L = 10$ and $d = 1$ (Scenario 1a), before focusing on the effects
 386 a reduction in L (to $L = 5$) has on the optimal solution (Scenario 1b) and then
 387 consider the effect of reducing the effectiveness per dollar in restriction effort d to 0.3
 388 (Scenario 1c).

389 In Scenario 1a (Fig 5(a)), we have that the marginal benefit of removal is always
 390 greater than the marginal cost (since $\frac{\partial Q}{\partial u_{rem}} < 0$ at $u_{rem} = 0$). Consequently, the
 391 optimal removal is maximum removal $u_{rem} = u_{remmax}$. This is to be expected, since
 392 removing an infected plant prevents not only losses from that infected plants (which
 393 are assumed to be equal to the removal cost, $L = C$) but also losses from secondary
 394 infections. Given that $R_0 > p(u_{ins})$ this additional loss from secondary infections is
 395 considerably greater than the potential loss that could result from the possibility of
 396 buying infected inputs when replacing plants that were subject to removal.

397 In Fig 5(a) and all other contour plots, the optimal level of restriction is
 398 determined by the line $MB_{ins} = MC_{ins}$. For Scenario 1a (Fig 5(a)), with no removal
 399 effort, the optimal level of restriction is around $u_{ins} = 1.2$. As the nursery increases its
 400 capacity to remove infected plants, it slowly reduces the optimal level of restriction.

401 Next, we consider the case where the revenue losses from infection are considerably
 402 lower (Scenario 1b, Fig 5(b)). Reducing the revenue losses from infection from $L = 10$
 403 to $L = 5$ has made removal less viable. It is better to leave an infected plant in the

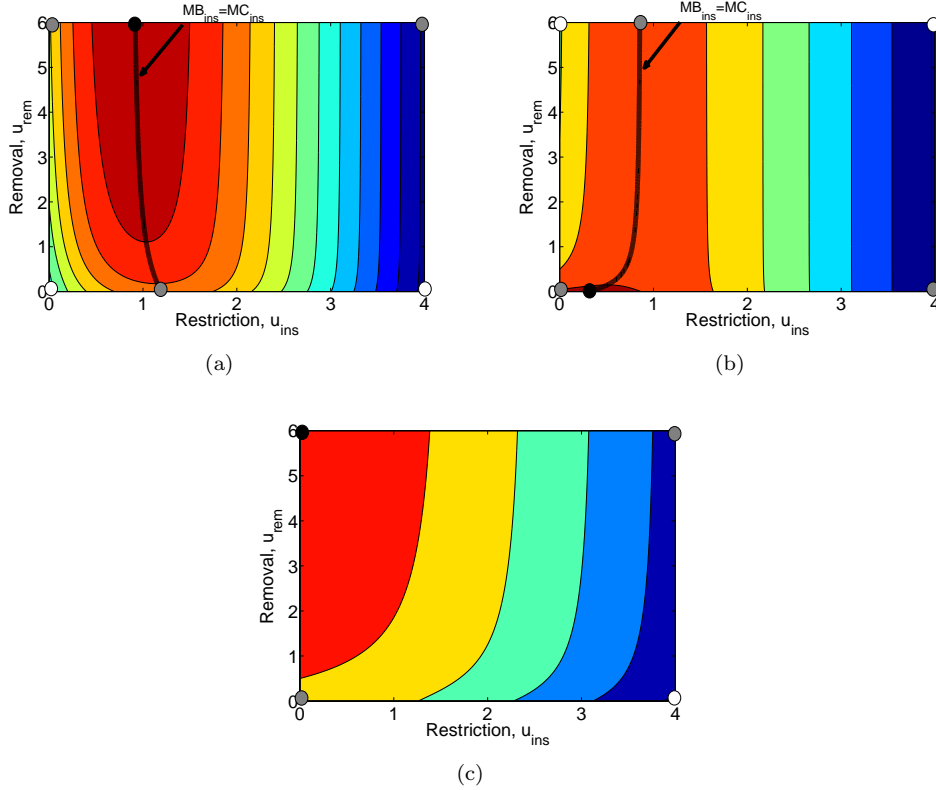


Figure 5. Contour plots of Q with respect to both removal and restriction for (a) Scenario 1a, (b) Scenario 1b and (c) Scenario 1c.

Red regions are the regions of lowest costs whereas blue regions signify highest costs. The black solid line represents $MB_{ins}=MC_{ins}$ (there are no lines for removal in this Scenario). Black dots are local minima, white dots are local maxima and grey dots are saddle points (points on the right boundary are local maxima/saddle point if we limit u_{ins} to regions in these figures). R_0 , L and d are given in Table 1. Other parameters: $C = 10$, $a = 0.2$ and $b = 0$.

404 nursery, because the costs of removing and replacing an infected plant is too expensive
 405 relative to the revenue loss associated to its lower net price.

406 Now, in contrast to Scenario 1a, Scenario 1c (Fig 5(b)) simulates a situation where
 407 restriction is more costly. This is represented by decreasing d from 1 to 0.3 and
 408 consequently spending an extra unit in restriction results in a reduction in infected
 409 inputs of $(1 - \exp^{-0.3}) * 100\% (\approx 26\%)$, considerably worse than the 63% in Scenario
 410 1a. This decrease in d has shifted the optimal restriction line where $MB_{ins}=MC_{ins}$ to
 411 the left, in this case the line is now to the left of the y-axis and thus beyond the
 412 realms of reality, and consequently restriction has become inviable. Thus the optimal
 413 strategy in Scenario 1c is maximum removal with no restriction (Fig 5(c)).

414 3.3.2. Scenario 2: High infectiousness

415 Increasing the basic reproduction number from $R_0 = 0.5$ (Scenario 1) to $R_0 = 5$
416 (Scenario 2) increases the complexity of the results.

417 When a disease is highly infectious, any small introduction of infected plants will
418 spread the disease through the nursery quickly. Consequently, investing in restriction
419 does not prevent the disease going through the plants growing in the nursery.
420 However, restriction does have a mild effect on disease prevalence when prevalence in
421 the nursery is high as the ‘cleaner’ inputted plants that replace those leaving the
422 nursery will have a mild rinsing effect. Thus, without removal effort, restriction is
423 often not viable (i.e. no restriction is optimal) when the disease is highly infectious.
424 This is particularly the case here when contrasting the viable restriction in Scenario 1a
425 (Fig 5(a) where $R_0 = 0.5$) and the inviable restriction in Scenario 2a (Fig 6(a)) when
426 there is no removal.

427 In Scenario 2a (Fig 6(a)) there are up to two local minima. We know from the
428 analytical results that optimal removal is either $u_{rem} = 0$ or $u_{rem} = u_{remmax}$.
429 Consequently we can argue about the importance of u_{remmax} by varying
430 $u_{rem} = u_{remmax}$ in the contour plots, following the $MB_{ins}=MC_{ins}$ line. If the nursery
431 capacity to remove is small, in particular such that u_{remmax} is below the intersection
432 of the $MB_{ins}=MC_{ins}$ and $MB_{rem}=MC_{rem}$ curves, then there is only one local (and
433 thus global) minimum, which is to do nothing and let the disease take its course. If
434 u_{remmax} is beyond the intersection, then there are two local minima, the
435 aforementioned ‘do nothing’ and $u_{rem} = u_{remmax}$ with the corresponding restriction
436 level given by $MB_{ins}=MC_{ins}$. The global minimum is one of these two local minima
437 and which one depends on the value of u_{remmax} ; if u_{remmax} is small enough that the
438 contour is either blue or green (below $u_{remmax} \approx 3.5$) then ‘do nothing’ is optimal,
439 whereas beyond $u_{remmax} \approx 3.5$ where the contours are yellow to red, then maximum
440 removal ($u_{rem} = u_{remmax}$) is the optimal strategy. Consequently, there is a great
441 range of values u_{remmax} where the optimal solution is to ‘do nothing’, that it is futile
442 to try and control the disease without being able to really get on top of it.

443 One particularly interesting result in Scenario 2a (Fig 6(a)) is the kink that occurs
444 in the $MB_{ins}=MC_{ins}$ curve. This kink occurs indistinguishably close to $R_0^p = 1$ since
445 the kink occurs around where the $MB_{ins}=MC_{ins}$ and $R_0^p = 1$ curves intersect. Below

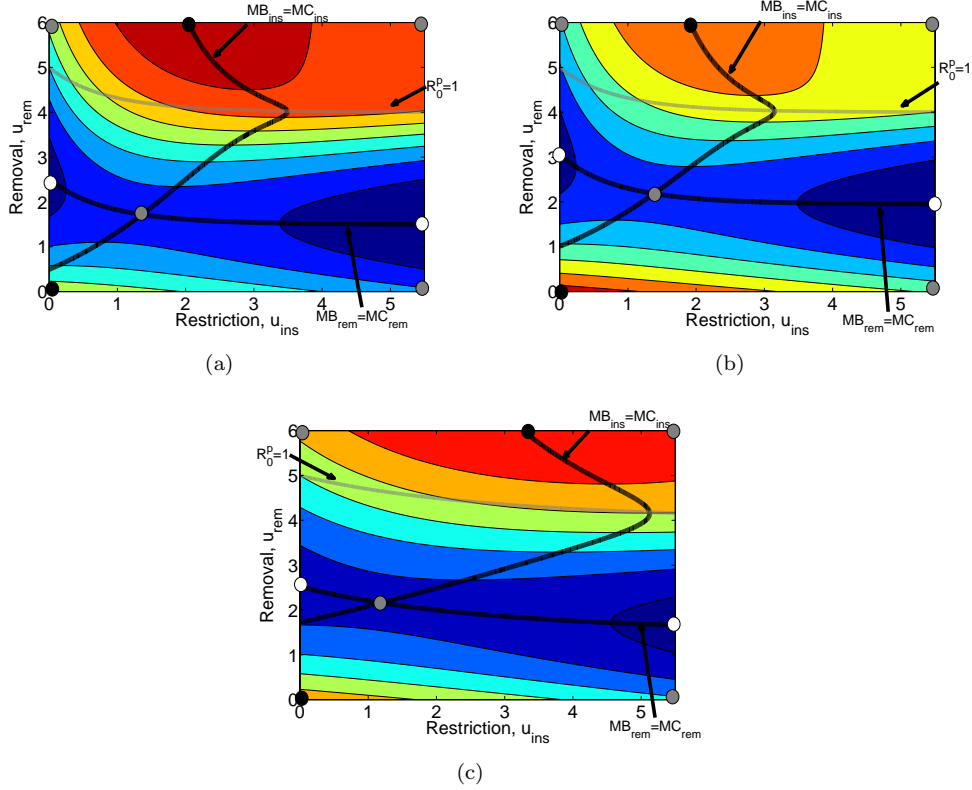


Figure 6. Contour plots of profit Q with respect to both removal and restriction for (a) Scenario 2a, (b) Scenario 2b and (c) Scenario 2c.

Red regions are the regions of lowest costs whereas blue regions signify highest costs. The black lines represent $MB_{ins}=MC_{ins}$ and $MB_{rem}=MC_{rem}$ whereas the grey line represents the values of (u_{ins}, u_{rem}) that correspond to $R_0^p = 1$. The dots have the same meaning as Fig 5(a). R_0 , L and d are given in Table 1. Other parameters are the same as Fig 5.

446 this kink, we have that increasing level of removal is linked with increasing level of
 447 restriction, i.e. removal and restrictions are complements. This occurs since restriction
 448 improves the effectiveness of removal as it reduces the chances that an infected plant,
 449 which has been removed, is replaced by another infected plant. However, above the
 450 kink, we have that increasing level of removal results in a decrease in the optimal level
 451 of restriction, i.e. they are substitutes. **This agrees with the final bullet point of**
 452 **the analytical results, where restriction and removal are complements**
 453 **when R_0 is large and u_{rem} is small, whereas restriction and removal are**
 454 **substitutes when u_{rem} is substantially larger than R_0 .**

455 Going from Scenario 2a to 2b (Fig 6(b)), there is a reduction in the loss in revenue
 456 from selling an infected plant from $L = 10$ to $L = 1$ (note that this is a considerably
 457 smaller revenue loss than in Scenario 1b). The effect of this small revenue loss in the

458 optimal effort of controlling the disease is relatively minor with respect to Scenario 2a;
 459 $MB_{ins}=MC_{ins}$ has shifted a little to the left, and thus the optimal level of restriction
 460 is reduced everywhere and $MB_{rem}=MC_{rem}$ has shifted a bit to the right and a little
 461 up. The consequence of the move in $MB_{rem}=MC_{rem}$ is that removal is also less viable
 462 everywhere. In particular, the intersection between these two lines that separates the
 463 two local minima has shifted up, increasing the region where there is only one local
 464 minimum; and consequently, ‘do nothing’ has become the optimal control irrespective
 465 to the value of u_{remmax} .

466 Notice that L has to be really small to achieve the result above. For $L = 5$, the
 467 global minimum is maximum removal as long as u_{remmax} is sufficiently above the kink
 468 around $R_0^p = 1$ (figure not given, use Fig 6(a) as guide). Conversely, a large increase in
 469 revenue losses, L , is needed to exclude ‘do nothing’ as a local optimal minimum; first,
 470 optimal restriction expenditure becomes positive for zero removal around $L = 25$ (i.e.
 471 $MB_{ins}=MC_{ins}$ intercepts the x-axis), and this ‘restriction only state’ becomes a local
 472 minimum. The ‘restriction only state’ remains a local minimum while the curves
 473 representing $MB_{ins}=MC_{ins}$ and $MB_{rem}=MC_{rem}$ intercept. This intercept disappears
 474 around $L = 45$, beyond which there is no ‘zero-removal’ local minimum. This means
 475 that even for large revenue losses, if the nursery capacity to remove is small (u_{remmax}
 476 small) then the nursery is very likely to be in the region where no expenditure in
 477 removal is optimal. This is because the disease will still spread through the nursery
 478 since R_0^p is still considerably larger than 1, making removal efforts futile.

479 Now, consider the case where restriction is less cost-effective as d is decreased to
 480 0.3 (Scenario 2c, Fig 6(c)). This decrease has a relatively minor effect on the removal
 481 line $MB_{rem}=MC_{rem}$ in Fig 6(c), the line keeps the same intercept with the y-axis and
 482 it is flatter than in Fig 6(a). This is predictable since decreasing cost-effectiveness
 483 means that more needs to be spent in restriction in order to have the same effect in
 484 the reduction of the probability of buying infected inputs. Likewise, the line of
 485 $MB_{ins}=MC_{ins}$ has (a) a higher intercept with the y-axis, making restriction less
 486 worthy if there is low removal, and (b) at the kink the expenditure on restriction has
 487 increased. The latter effect is due to the reduction in the cost-effectiveness (essentially
 488 an increase in the price of a 50% reduction in infected inputs) which does reduce
 489 restriction effort, but it does increase total spending on restriction.

490 4. Discussion and Conclusions

491 In this paper, we have analysed the prevention and control management options
492 available to a nursery owner in order to minimise the impacts of an infectious disease
493 that may spread within the nursery. To this end, we derived a bioeconomic model of a
494 plant nursery, where the manager can opt either to restrict the proportion of infected
495 plant material coming into the nursery (prevention), or remove infected plants within
496 the nursery (control), or a combination of both strategies. We assume that there is an
497 upper limit on removal effort. Our analytical results show that (a) if infected inputs
498 are always coming into the nursery, the disease would persist in the nursery, and will
499 approach a unique endemic steady state (Section 3.1.2 and Figure 4); (b) the optimal
500 removal is either maximum removal (i.e. the upper limit in removal efforts given the
501 nursery's capacity) or no removal, as long as restriction efforts are optimally allocated,
502 i.e. where the marginal cost of restriction equals its marginal benefit in terms of
503 disease damages avoided (Section 3.2); (c) optimal restriction expenditure increase
504 with both the revenue losses for selling mature infected plants and costs of removal;
505 while maximal removal is more likely to be optimal if either revenue infection losses
506 increase or removal costs decrease (Section 3.2); (d) since any removed infected plant
507 stock needs to be replaced buying new plant inputs, which could potentially be
508 infected, the manager can increase the effectiveness of removal effort by increasing
509 restriction effort (see expressions of R_0^p and i^* in Section 3.1.2).

510 The numerical analysis of the Scenarios (summarised in Table 1) with varying
511 conditions in the level of infectiousness of the disease, damages to the nursery, and
512 cost-effectiveness of management efforts, highlights three relevant results for private
513 biosecurity decisions. First, results indicate that it is optimal to spend on maximum
514 removal efforts unless the revenue losses from selling infected mature plants are
515 considerable lower than the cost of removal (especially for highly infectious diseases,
516 e.g. Scenario 2).

517 Secondly, if the capacity to remove infected plants is very limited, due for example
518 to temporal or monetary constrains, it may be optimal to 'do nothing' (again,
519 particularly for highly infectious diseases, Scenario 2). It is only worth removing
520 infected plants if the efforts applied can limit the expansion of the disease through

521 secondary infections within the nursery, otherwise removal resources could be waste; it
522 is not worthwhile removing an infected plant if the replaced plant will likely become
523 infected. The private benefits of removal efforts in curbing the disease has therefore
524 threshold properties. Benefits can only be achieved once at least a minimum amount
525 has been contributed to their production. This property on removal efforts is expected
526 to affect the probability of cooperating [e.g. 45, 46], when strategic decisions among
527 private agents is relevant to limit the probability of outbreaks [e.g. 31, 47].

528 A third result is the finding of synergies between restriction and removal strategies,
529 which are determined by the reproduction number, i.e. how contagious a disease is and
530 could be spread through trade. This contributes to previous existing literature that
531 only focus on substitutionary effects between prevention and control. For example,
532 Olson and Roy[48] examine the conditions under which the optimal policy relies solely
533 on either prevention or control. Kim *et al.*[49] examine the optimal combination of
534 pre-discovery prevention, post-discovery prevention and post-discovery control where
535 the discovery time is stochastic, and find that post-discovery prevention and control
536 are substitutes. Leung *et al.*[22] consider that if there is expensive control activities,
537 this reduces social welfare at the post-invasion state, and consequently higher social
538 welfare can be achieved from avoiding invasion, and substituting control by prevention
539 efforts. Similarly, Finnoff *et al.* [24] conclude that a risk averse agent would substitute
540 more prevention expenditures with control policies when compared to a risk neutral
541 agent. Here, we found that the optimal level of restriction is complementary with
542 removal efforts if the disease is beyond the nursery owner's ability to limit its spread.
543 The underlying reason for this is that, restriction measures may not be very effective
544 in the case of highly infectious diseases (Scenario 2), since some infected plants
545 materials will always get past the restriction regime, and once infected plants are in
546 the nursery the disease will spread fast within the nursery. In those situations, if the
547 manager increases the level of effort in removing infected plants, the disease becomes
548 more manageable, and consequently making expenditures in restriction measures more
549 effective. In addition, increased efforts on restriction makes also removal more effective,
550 reducing the probability of buying infected inputs when the nursery owner has to buy
551 new stock to replace those infected plants that were removed. Consequently, removal
552 and restriction efforts are complementary for highly infected diseases.

553 This phenomenon where ‘prevention’ and ‘cure’ are complementary has been found
554 in the human health literature in [50, 51]. Hennessy *et al.*[51] argue that for
555 ‘prevention’ and ‘cure’ being complements is that increasing prevention reduces the
556 chance that cured individuals become sick again and thus improving the long term
557 benefit of curing sick individuals. This argument is analogous to the reasons that can
558 explain why restriction improves the effectiveness of removal in Scenario 2, as the
559 replacement of a removed infected plant with an infected plant can be seen as
560 (instantaneous) reinfection.

561 We also show that this complementary relationship between prevention and control
562 continues as removal level increase until around $R_0^p = 1$. Beyond this point the disease
563 no longer is able to spread through the nursery and instead relies on the constant
564 introduction of infected plant inputs to persist in the nursery. In this case, the disease
565 could be manageable through the removal programme, and the nursery owner can
566 choose whether to remove it once it is in the nursery or prevent it from entering the
567 nursery. This means, restriction and removal efforts are substitutes, akin to the classic
568 ‘prevention vs cure’ argument.

569 However, it should be noted that the analysis in this paper is based on the long
570 term dynamics of the disease and decision making, thus our work fits more the
571 endemic stage of an infection with the nursery being subject to continual invasion
572 pressure. Consequently, it neglects the epidemic/invasion stage, and uncertain benefits
573 from delaying the spread of the disease through prevention and/or surveillance during
574 this stage [e.g. 19, 25]. Moreover, we also recognise that many nurseries work on a
575 shorter term basis than used in this model. For example, some nurseries are seasonal
576 and only have a generation or two of plants in the nursery for one season before an
577 annual reset of the nursery, with new plants stock. In this case, a steady state might
578 not be appropriate analysis as not enough time has occurred for a steady state to be
579 reached. Following the above literature, in cases like those in Scenario 2 with highly
580 infectious diseases, restriction and removal may be more viable in the early stages of
581 disease introduction (unlike the long term) since they can delay the inevitable disease
582 spreading through the nursery. However, even in shorter time-scales,
583 equilibrium-based analysis form a strong baseline for understanding optimal decisions.

584 In the model derivation process we assumed that the nursery stock is fixed (i.e. the

nursery is always full). This is not always true, especially if seasonal effects (like
weather or seasonal demand) occur or if the nursery owner reduces the size of the
nursery as a disease management tool. During periods with a reduced nursery stock,
the basic reproductive number R_0 is reduced (since the disease is density dependent)
as is the cost-effectiveness of restriction, ‘ d ’. The reduction in R_0 means the disease
will spread less within the nursery and thus is easier to control by removal.
Consequently, the constant full nursery assumption used in this paper gives an upper
limit to the extent of the disease will spread and thus a worst case scenario in terms of
uncontrolled damages from a pathogen. On top of that, the reduction on R_0 from a
lower N reduces the range of u_{rem} where restriction and removal are complements. On
the other hand, the reduction in the cost-effectiveness of restriction would result in a
less stringent restriction regime (i.e. an increase in the proportion of infected plant
inputs, $p(u_{ins})$), akin to what is found when comparing Scenarios 1a and 2a with
Scenarios 1c and 2c.

In this paper, we have assumed the disease is an SI disease, i.e. each plant is either
susceptible or infected and there is no recovery from the disease. This was for
simplicity and generality. However, many plant diseases have recovery, latency,
asymptomatic infection and immunity, as well as free-living stages in the environment
(i.e. in the soil or water). The presence of asymptomatic and latent infected plant
inputs undermines the owner’s ability to restrict infected inputs coming into the
nursery since identifying infected plants material inputs becomes much more complex
or even impossible if no symptoms of infection or clear evidence of pathogens are
present. In addition, our analysis only focuses on diseases that can only enter the
nursery via infected plant material inputs (i.e. through plant trade). However, for
many different nurseries, pathogens and pests get into the nursery through a number
of different pathways. In particular, contaminated water is often the reason for
Phytophthora and other pathogens getting into plant nurseries [52, and references
therein]. We suspect that in this situation, restriction strategies that focus on
inspecting plant inputs would have a limited effect on preventing the diseases, which
would reduce their cost-effectiveness and therefore their optimal level of provision.

The level of restriction in this paper depends greatly on the choice of the function
 $p(u_{ins})$, the proportion of infected plant material inputs that are infected for a given

617 level of restriction. In this paper, we used an exponentially decreasing function to
618 obtain numerical results since it was the simplest function that satisfies the desired
619 properties of $p(u_{ins})$ (i.e. which, in short, is monotonic decreasing of u_{ins}). This
620 function has the property that the first dollar spent on restriction is always the most
621 effective, and that each dollar spent has a smaller effect on $p(u_{ins})$ than the previous
622 dollar. This property would not necessarily be appropriate in several cases. For
623 example, functions where a small investment in restriction has little effect and a
624 substantial investment that more has to spent for a restriction regime to start to have
625 a noticeable effect on the proportion of infected plant materials coming in could be
626 more appropriate if substantial funds are needed for effective levels of knowledge,
627 labour, machinery and skills to be maintained. A suggested simple function that could
628 provide useful incite into management satisfies this property is $(a - b) \exp^{-du_{ins}^2} + b$ (in
629 which case the most cost-effective level of restriction is at $u_{ins} = (2d)^{-1/2}$).

630 Finally, note that this paper deals with one disease of concern for the nursery
631 owner to control. Generally, a nursery owner has a multitude of diseases to be
632 concerned about. For example, the tomato *Solanum lycopersicum* is known to be a
633 host for over 500 different pests and pathogens [53]. Likewise, a nursery can have
634 many pathogens present. For example, at least 13 different species of *Phytophthora*
635 were found in the irrigation water at three nurseries in northern Germany in 1995
636 [54, 55]. Likewise, in Bavaria in 2002, there were five different species of *Phytophthora*
637 found in the soil around a single open-planted alder seedling [T.Jung, LWF, D-85354
638 Freising, personal communication cited in 55]. With a multitude of diseases to
639 manage, a common optimal strategy on restriction and removal would be needed, a
640 strategy that would likely differ from the strategy of each of the diseases in isolation.

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Appendix A. Optimal solution with respect to u_{rem} : ‘all or nothing’

To find out what the optimal solutions with respect to u_{rem} , we need to investigate:

$$\frac{\partial Q}{\partial u_{rem}} = (L + Cu_{rem}) \frac{\frac{\partial M}{\partial u_{rem}} + \frac{2M \frac{\partial M}{\partial u_{rem}}}{2\sqrt{M^2 + 4R_0 p(u_{ins})}}}{2R_0} + C \frac{M + \sqrt{M^2 + 4R_0 p(u_{ins})}}{2R_0} = 0, \quad (\text{A.1})$$

where $M(u_{ins}, u_{rem}) = R_0 - 1 - (1 - p(u_{ins}))u_{rem}$. First, we need to manipulate this into something more manageable.

$$\frac{\partial Q}{\partial u_{rem}} = -\frac{(L + Cu_{rem})(1 - p(u_{ins}))}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) + \frac{C}{2R_0} \left(M + \sqrt{M^2 + 4R_0 p(u_{ins})} \right) \quad (\text{A.2})$$

$$= -\frac{C}{2R_0} \left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) \left(1 + \frac{M}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) - \left(M + \sqrt{M^2 + 4R_0 p(u_{ins})} \right) \right) \quad (\text{A.3})$$

$$= -\frac{C}{2R_0 \sqrt{M^2 + 4R_0 p(u_{ins})}} \left(\left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) - 4R_0 p(u_{ins}) \right) \quad (\text{A.4})$$

Consequently, solutions of $\frac{\partial Q}{\partial u_{rem}} = 0$ are solutions of

$\left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) - 4R_0 p(u_{ins}) = 0$. Now, if such solutions exist and are admissible, we need to find out if one of these solution is a maximum with respect u_{rem} . To do so, we need to look at the second derivative.

$$\begin{aligned} \frac{\partial^2 Q}{\partial u_{rem}^2} &= -\frac{C}{2R_0} \frac{\partial M}{\partial u_{ins}} \frac{\partial}{\partial M} \left(\frac{1}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) \overbrace{\left(\left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) - 4R_0 p(u_{ins}) \right)}^{=0} \\ &\quad - \frac{C}{2R_0 \sqrt{M^2 + 4R_0 p(u_{ins})}} \left((1 - p(u_{ins})) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) - \frac{\partial M}{\partial u_{ins}} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) \right) \\ &\quad + \left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) \frac{\partial M}{\partial u_{ins}} \frac{\partial}{\partial M} \left(\sqrt{M^2 + 4R_0 p(u_{ins})} \right) \end{aligned} \quad (\text{A.5})$$

$$\begin{aligned} &= -\frac{C}{2R_0 \sqrt{M^2 + 4R_0 p(u_{ins})}} \left(2(1 - p(u_{ins})) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) \right. \\ &\quad \left. - (1 - p(u_{ins})) \left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(1 + \frac{M}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) \right) \end{aligned} \quad (\text{A.6})$$

$$\begin{aligned} &= -\frac{C(1 - p(u_{ins}))}{2R_0(M^2 + 4R_0 p(u_{ins}))} \left(2 \left(M^2 + 4R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) \right. \\ &\quad \left. - \left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) \right) \end{aligned} \quad (\text{A.7})$$

$$\begin{aligned} &= -\frac{C(1 - p(u_{ins}))}{2R_0(M^2 + 4R_0 p(u_{ins}))} \left(2 \left(M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) \right. \\ &\quad \left. - \overbrace{\left(\left(\left(\frac{L}{C} + u_{rem} \right) (1 - p(u_{ins})) - M \right) \left(\sqrt{M^2 + 4R_0 p(u_{ins})} + M \right) \right)}^{=0} - 4R_0 p(u_{ins}) \right) \end{aligned} \quad (\text{A.8})$$

$$= -\frac{C(1 - p(u_{ins}))}{R_0(M^2 + 4R_0 p(u_{ins}))} \left(M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) \quad (\text{A.9})$$

If $M > 0$, then $\frac{\partial^2 Q}{\partial u_{rem}^2} < 0$ and thus all internal solutions are local maxima with respect to u_{rem} . It is not completely clear if this is the case for $M < 0$ so instead look to find the value of M where $M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})}$ has its minimum. So we look at the properties of solutions of

$$\frac{\partial}{\partial M} \left(M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) = 0.$$

$$\frac{\partial}{\partial M} \left(M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) = 2M + \sqrt{M^2 + 4R_0 p(u_{ins})} + \frac{M^2}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \quad (\text{A.10})$$

$$= \frac{2}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \left(M^2 + 2R_0 p(u_{ins}) + M \sqrt{M^2 + 4R_0 p(u_{ins})} \right) = 0 \quad (\text{A.11})$$

Solutions of this satisfy $M = -\frac{M^2 + 2R_0 p(u_{ins})}{\sqrt{M^2 + 4R_0 p(u_{ins})}}$. Substituting this into

$M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})}$ gives:

$$\begin{aligned}
& -\frac{M^2 + 2R_0p(u_{ins})}{\sqrt{M^2 + 4R_0p(u_{ins})}} \left(-\frac{M^2 + 2R_0p(u_{ins})}{\sqrt{M^2 + 4R_0p(u_{ins})}} + \sqrt{M^2 + 4R_0p(u_{ins})} \right) + 2R_0p(u_{ins}) \\
& = -\frac{M^2 + 2R_0p(u_{ins})}{M^2 + 4R_0p(u_{ins})} \left(-(M^2 + 2R_0p(u_{ins})) + M^2 + 4R_0p(u_{ins}) \right) + 2R_0p(u_{ins}) \quad (\text{A.12}) \\
& = 2R_0p(u_{ins}) \left(1 - \frac{M^2 + 2R_0p(u_{ins})}{M^2 + 4R_0p(u_{ins})} \right) > 0
\end{aligned}$$

and thus $M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})} > 0$ always and thus $\frac{\partial^2 Q}{\partial u_{rem}^2} > 0$ and thus internal solutions are always local maxima with respect to u_{rem} . As there is no internal minimum with respect to u_{rem} , the global minimum must occur on the boundary, either at $u_{rem} = 0$ or $u_{rem} = u_{remmax}$. If $\frac{\partial Q}{\partial u_{rem}} < 0$ at $u_{rem} = 0$ then $u_{rem} = 0$ is a local (global) maximum and $u_{rem} = u_{remmax}$ is the global minimum. Conversely, if $\frac{\partial Q}{\partial u_{rem}} > 0$ at $u_{rem} = u_{remmax}$ then $u_{rem} = u_{remmax}$ is a local (global) maximum and thus $u_{rem} = 0$ is a global minimum. If $\frac{\partial Q}{\partial u_{rem}} > 0$ at $u_{rem} = 0$ and $\frac{\partial Q}{\partial u_{rem}} < 0$ at $u_{rem} = u_{remmax}$, then you have must compare Q for $u_{rem} = 0$ and $u_{rem} = u_{remmax}$ since both are local minima.

Appendix B. Optimal control with respect to restriction u_{ins} : ‘do something or do nothing’

We need to find out the global minimum with respect to restriction u_{ins} by analysing:

$$\frac{\partial Q}{\partial u_{ins}} = (L + Cu_{rem}) \frac{\frac{\partial M}{\partial u_{ins}} + \frac{2M \frac{\partial M}{\partial u_{ins}} + 4R_0 \frac{\partial p(u_{ins})}{\partial u_{ins}}}{2\sqrt{M^2 + 4R_0p(u_{ins})}}}{2R_0} + 1 = 0. \quad (\text{B.1})$$

where $M(u_{ins}, u_{rem}) = R_0 - 1 - (1 - p(u_{ins}))u_{rem}$. First, we will look at the second partial derivative to see if $\frac{\partial Q}{\partial u_{ins}}$ is an increasing or decreasing function of u_{ins} :

$$\frac{\partial^2 Q}{\partial u_{ins}^2} = \frac{\partial^2 p(u_{ins})}{\partial u_{ins}^2} \frac{(L + Cu_{rem})}{2R_0} \left(u_{rem} + \frac{Mu_{rem} + 2R_0}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \right) + \left(\frac{\partial p(u_{ins})}{\partial u_{ins}} \right)^2 \frac{(L + Cu_{rem})}{2R_0} \left(\frac{-2R_0(Mu_{rem} + 2R_0)}{(M^2 + 4R_0 p(u_{ins}))^{\frac{3}{2}}} \right) \quad (\text{B.2})$$

$$= \frac{\partial^2 p(u_{ins})}{\partial u_{ins}^2} \frac{L + Cu_{rem}}{2R_0} \left(u_{rem} + \frac{(Mu_{rem} + 2R_0)(M^2 + 4R_0 p(u_{ins})) - 2R_0 \frac{\left(\frac{\partial p}{\partial u_{ins}}\right)^2}{\partial u_{ins}^2} (Mu_{rem} + 2R_0)}{(M^2 + 4R_0 p(u_{ins}))^{\frac{3}{2}}} \right) \quad (\text{B.3})$$

$$= \frac{\partial^2 p(u_{ins})}{\partial u_{ins}^2} \frac{L + Cu_{rem}}{2R_0} \left(u_{rem} + \frac{M^2 + 4R_0 p(u_{ins}) - 2R_0 \frac{\left(\frac{\partial p}{\partial u_{ins}}\right)^2}{\partial u_{ins}^2}}{M^2 + 4R_0 p(u_{ins})} \frac{Mu_{rem} + 2R_0}{\underbrace{\sqrt{M^2 + 4R_0 p(u_{ins})}}_{\text{always } > -u_{rem}}} \right) \quad (\text{B.4})$$

Now, since we do not have sufficient knowledge on the properties of $\frac{\partial^2 p}{\partial u_{ins}^2}$ in general, we will continue with $p(u_{ins}) = b + (a - b) \exp(-du_{ins})$. Thus

$$\frac{\partial p}{\partial u_{ins}} = -d(a - b) \exp(-du_{ins}) = -d(p(u_{ins}) - b) \text{ and}$$

$$\frac{\partial^2 p}{\partial u_{ins}^2} = -d \frac{\partial p}{\partial u_{ins}} = d^2(a - b) \exp(-du_{ins}) = d^2(p(u_{ins}) - b). \text{ Armed with this, we have:}$$

$$\frac{\partial^2 Q}{\partial u_{ins}^2} = \frac{(L + Cu_{rem})d^2(p(u_{ins}) - b)}{2R_0} \left(\underbrace{u_{rem} + \frac{\overbrace{M^2 + 2R_0(p(u_{ins}) + b)}^{\in(0,1)}}{M^2 + 4R_0 p(u_{ins})} \frac{\overbrace{Mu_{rem} + 2R_0}^{\text{always } > -u_{rem}}}{\sqrt{M^2 + 4R_0 p(u_{ins})}}}_{>0} \right) \quad (\text{B.5})$$

$$> 0 \text{ when } L + Cu_{rem} > 0 \quad (\text{B.6})$$

Firstly, we note that if $L + Cu_{rem} \leq 0$ (which could be true if $L < 0$), there are no internal solutions from possible for Equation (17) from the main text and we have

$\frac{\partial Q}{\partial u_{ins}}$ is monotonically increasing to -1. Hence, $\frac{\partial Q}{\partial u_{ins}} < 0$ always and thus zero restriction is always the best (a disease that is beneficial should not be restricted). For $L + Cu_{rem} > 0$, we have that $\frac{\partial Q}{\partial u_{ins}}$ is monotonically increasing (to 1 as $u_{ins} \rightarrow \infty$). In other words, increasing restriction has even diminishing returns, reducing the marginal benefit, whereas the marginal cost remains the same. Given we have that $\frac{\partial Q}{\partial u_{ins}}$ is monotonically increasing to 1 (and is continuous), we know that there exists one and only one admissible solution with respect to u_{ins} (for fixed u_{rem}) if $\frac{\partial Q}{\partial u_{ins}} < 0$ at

$u_{ins} = 0$ and that this solution is a global minimum with respect to u_{ins} , i.e. the optimal control involves some restriction. Otherwise, $\frac{\partial Q}{\partial u_{ins}} \geq 0$ at $u_{ins} = 0$, there is no internal solution and the global minimum with respect to u_{ins} is at $u_{ins} = 0$, i.e. no restriction is optimal.

If such solutions do not exist within admissible controls ($u_{rem} \in [0, u_{remmax}]$ and $u_{ins} \geq 0$), we need to pick the minimising values on the boundary, i.e. if $\frac{\partial Q}{\partial u_{ins}} > 0$ at $u_{ins} = 0$, then either $u_{ins} = 0$ and $u_{ins} = \infty$ are the global maximum. However, since $\frac{\partial Q}{\partial u_{ins}} \rightarrow 1$ as $u_{ins} \rightarrow \infty$ (because $p(u_{ins})$ is converging to b and thus $\frac{\partial p(u_{ins})}{\partial u_{ins}} \rightarrow 0$), $u_{ins} = \infty$ is always a local maximum and thus $u_{ins} = 0$ is the global minimum, i.e. the cost minimising strategy, when $\frac{\partial Q}{\partial u_{ins}} > 0$ at $u_{ins} = 0$.

Appendix C. Linking dynamic and stationary approaches

Taking Equation (6) and following the rescaling and rearrangement that occur between Equation (7) and (9) leads to:

$$\min_{u_{ins}, u_{rem}} \int_0^{\hat{T}} e^{-\hat{r}t} ((L + Cu_{rem})i + u_{ins}) dt \quad (\text{C.1})$$

where $\hat{T} = T\delta$ and $\hat{r} = \frac{r}{\delta}$ (henceforth, we will drop these hats for simplicity, being consistent with what was done in the main text). First, we establish and analyse the Hamiltonian of Equations (9) and (10). This Hamiltonian is:

$$H = e^{-rt} ((-L - Cu_{rem})i - u_{ins}) + \lambda (p(u_{ins})(1 + u_{rem}i) - i - u_{rem}i + R_0(1 - i)i). \quad (\text{C.2})$$

Consequently, the adjoint equation is:

$$\frac{d\lambda}{dt} = -\frac{\partial H}{\partial i} = -(e^{-rt}(-L - Cu_{rem}) + \lambda(p(u_{ins})u_{rem} - 1 - u_{rem} + R_0(1 - 2i))). \quad (\text{C.3})$$

The optimality conditions for u_{ins} and u_{rem} are:

$$\frac{\partial H}{\partial u_{ins}} = -e^{-rt} + \lambda \left(\frac{\partial p(u_{ins})}{\partial u_{ins}} (1 + u_{rem}i) \right) = 0 \quad (\text{C.4})$$

and

$$\frac{\partial H}{\partial u_{rem}} = i(\lambda(p(u_{ins}) - 1) - Ce^{-rt}) = 0, \quad (\text{C.5})$$

respectively.

To link the solutions in this paper to those of this Hamiltonian, we will assume an infinite time interval, and treat u_{rem} , u_{ins} as constants. On top of this, we will insert the steady state value of i^* from Equation (11) given from the population dynamics. Rearranging (C.4) gives:

$$\lambda = \frac{e^{-rt}}{\left(\frac{\partial p(u_{ins})}{\partial u_{ins}}(1 + u_{rem}i)\right)}. \quad (\text{C.6})$$

Inserting this into (C.3) gives:

$$\frac{d\lambda}{dt} = e^{-rt} \left(L + Cu_{rem} + \frac{p(u_{ins})u_{rem} - 1 - u_{rem} + R_0(1 - 2i)}{\frac{\partial p(u_{ins})}{\partial u_{ins}}(1 + u_{rem}i)} \right). \quad (\text{C.7})$$

From this, using the constant u_{rem} , u_{ins} and i^* assumption and assuming $\lambda = 0$ at infinity, gives:

$$\lambda = -\frac{1}{r}e^{-rt} \left(L + Cu_{rem} + \frac{p(u_{ins})u_{rem} - 1 - u_{rem} + R_0(1 - 2i)}{\frac{\partial p(u_{ins})}{\partial u_{ins}}(1 + u_{rem}i)} \right). \quad (\text{C.8})$$

Using the two expressions for λ (C.6) and (C.8), we get:

$$\frac{1}{\frac{\partial p(u_{ins})}{\partial u_{ins}}(1 + u_{rem}i)} = -\frac{1}{r} \left(L + Cu_{rem} + \frac{p(u_{ins})u_{rem} - 1 - u_{rem} + R_0(1 - 2i)}{\frac{\partial p(u_{ins})}{\partial u_{ins}}(1 + u_{rem}i)} \right). \quad (\text{C.9})$$

Inserting $i^* = \frac{M + \sqrt{M^2 + 4p(u_{ins})R_0}}{2R_0}$, where $M = R_0 - 1 - (1 - p(u_{ins}))u_{rem}$, and with a little rearranging, we arrive at:

$$r = - \left((L + Cu_{rem}) \frac{\partial p(u_{ins})}{\partial u_{ins}} \left(1 + u_{rem} \frac{M + \sqrt{M^2 + 4pR_0}}{2R_0} \right) + \sqrt{M^2 + 4pR_0} \right). \quad (\text{C.10})$$

Dividing everything by $-\sqrt{M^2 + 4p(u_{ins})R_0}$ and rearranging gives:

$$-\frac{r}{\sqrt{M^2 + 4p(u_{ins})R_0}} = 1 - \left(-\frac{(L + Cu_{rem}) \frac{\partial p(u_{ins})}{\partial u_{ins}}}{2R_0} \left(u_{rem} + \frac{Mu_{rem} + 2R_0}{\sqrt{M^2 + 4R_0p(u_{ins})}} \right) \right). \quad (\text{C.11})$$

Notice that the right hand side is $\frac{dQ}{du_{ins}} = MC_{ins} - MB_{ins}$ from Equation (14). Thus

for zero discounting ($r = 0$), $\frac{dQ}{du_{ins}} = 0$ gives the optimal restriction, whereas for a positive discounting rate ($r > 0$), the optimal restriction satisfies $\frac{dQ}{du_{ins}} = -\frac{r}{\sqrt{M^2 + 4R_0p(u_{ins})}}$. However, since $\frac{dQ}{du_{ins}}$ is monotonically increasing function, we know that increasing the discount rate (r) would lower the optimal level of restriction. This effect is very dependent on how long the plant is expected to be in the nursery due to the time rescaling (i.e. since $\hat{r} = \frac{r}{\delta}$). If the average plant stay is short (i.e. weeks to months) then this discounting effect is negligible, whereas for longer period (i.e. years), this term becomes larger, having more impact on the optimal restriction.

Moving on to optimal removal, (C.5) is generally never satisfied, and instead the optimal removal is a ‘bang–bang’ control (i.e. all or nothing) which is consistent with the static analysis. Consequently, the optimal solution is either $u_{rem} = 0$ or $u_{rem} = u_{remmax}$, which depends on the sign of $\lambda(p(u_{ins}) - 1) - Ce^{-rt}$.

To determine the sign, we will focus on the threshold $\lambda(p(u_{ins}) - 1) - Ce^{-rt} = 0$. Substituting Equation C.6 and rearranging gives:

$$C \frac{\partial p(u_{ins})}{\partial u_{ins}} (1 + u_{rem}i) = -(1 - p(u_{ins})). \quad (\text{C.12})$$

Now, rearranging Equation (C.9) and inserting the steady state value of i^* from Equation (11) gives

$$\frac{\partial p(u_{ins})}{\partial u_{ins}} (1 + u_{rem}i) = -\frac{r + \sqrt{M^2 + 4p(u_{ins})R_0}}{L + Cu_{rem}}. \quad (\text{C.13})$$

Substituting this into C.12 and arranging gives

$$Cr = (L + Cu_{rem})(1 - p(u_{ins})) - C\sqrt{M^2 + 4p(u_{ins})R_0}. \quad (\text{C.14})$$

Multiplying by $\frac{-1}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0p(u_{ins})}}\right)$ we arrive at:

$$-\frac{rC}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0p(u_{ins})}}\right) = \frac{C}{2R_0} (M + \sqrt{M^2 + 4p(u_{ins})R_0}) - \frac{(L + Cu_{rem})(1 - p(u_{ins}))}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0p(u_{ins})}}\right). \quad (\text{C.15})$$

This of condition is analogous with the static problem, with the right hand side being $\frac{dQ}{du_{rem}} = MC_{rem} - MB_{rem}$ from Equation (13).

This alone does not give the global optimal since there are two λ 's to compare, one where $u_{rem} = 0$, the other where $u_{rem} = u_{remmax}$. In cases where $\lambda(u_{rem} = 0)(p(u_{ins}) - 1) - Ce^{-rt} < 0$ but $\lambda(u_{rem} = u_{remmax})(p(u_{ins}) - 1) - Ce^{-rt} > 0$, a comparison in terms of profit must be made, which is analogous to the two local optima solutions found in the static solutions. Again, like with restriction, we have that no discounting gives the same result, and increasing the discount rate makes $u_{rem} = u_{remmax}$ less likely to be globally optimal.

References

- [1] P. K. Anderson, A. A. Cunningham, N. G. Patel, F. J. Morales, P. R. Epstein, P. Daszak, Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers, *Trends in Ecology & Evolution* 19 (10) (2004) 535–544.
- [2] J. K. Waage, J. D. Mumford, Agricultural biosecurity, *Philosophical Transactions of the Royal Society B* 363 (2008) 863–876.
- [3] C. Perrings, S. Burgiel, M. Lonsdale, H. Mooney, M. Williamson, International cooperation in the solution to trade-related invasive species risks., *Conservation Ecology* 1195 (2010) 198–212.
- [4] P. E. Hulme, Invasive species challenge the global response to emerging diseases, *Trends in Parasitology* 30 (2014) 267–270.
- [5] S. Dalmazzone, S. Giaccaria, Economic drivers of biological invasion: A worldwide, bio-geographic analysis., *Ecological Economics* 105 (2014) 154–165.
- [6] M. Pautasso, G. Aas, V. Queloz, O. Holdenrieder, European ash (*Fraxinus excelsior*) dieback- a conservation biology challenge., *Biological Conservation* 158 (2013) 37–49.
- [7] C. Brasier, J. Webber, Plant pathology: Sudden larch death., *Nature* 466 (2010) 824–825.

- [8] D. M. Rizzo, M. Garbelotto, J. M. Davidson, G. W. Slaughter, S. T. Koike, *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in california., *Plant Disease* 86 (2002) 205–214.
- [9] A. Santini, L. Ghelardini, C. De Pace, M. L. Desprez-Loustau, P. Capretti, A. Chandelier, T. Cech, D. Chira, S. Diamandis, T. Gaitniekis, J. Hantula, O. Holdenrieder, L. Jankovsky, T. Jung, D. Jurc, T. Kirisits, A. Kunca, V. Lygis, M. Malecka, B. Marcais, S. Schmitz, J. Schumacher, H. Solheim, A. Solla, I. Szabò, P. Tsopelas, A. Vannini, A. M. Vettraino, J. Webber, S. Woodward, J. Stenlid, Biogeographical patterns and determinants of invasion by forest pathogens in europe, *New Phytologist* 197 (2013) 238–250.
- [10] A. M. Liebhold, E. G. Brockerhoff, L. J. Garrett, J. L. Parke, K. O. Britton, Live plant imports: the major pathway for forest insect and pathogen invasions of the us, *Frontiers in Ecology and the Environment* 10 (2012) 135–143.
- [11] T. J. Stohlgren, J. L. Schnase, Risk analysis for biological hazards: what we need to know about invasive species, *Risk Analysis* 26 (2006) 163–173.
- [12] L. J. Olson, The economics of terrestrial invasive species: A review of the literature, *Agricultural and Resource Economics Review* 35 (2006) 178–194.
- [13] G. Marbuah, I.-M. Gren, B. McKie, Economics of harmful invasive species: A review, *Diversity* 6 (2014) 500–523.
- [14] C. McAusland, C. Costello, Avoiding invasives: trade-related policies for controlling unintentional exotic species introduction, *Journal of Environmental Economics and Management* 48 (2004) 954–977.
- [15] P. R. Mérel, C. A. Carter, A second look at managing import risk from invasive species, *Journal of Environmental Economics and Management* 56 (2008) 286–290.
- [16] R. P. Keller, M. R. Springborn, Closing the screen door to new invasions, *Conservation Letters* 285 (2014) 285–292.
- [17] M. R. Springborn, R. P. Keller, S. Elwood, C. M. Romagosa, C. Zambrana-Torrel, P. Daszak, Integrating invasion and disease in the risk assessment of live bird trade, *Diversity and Distributions* 21 (2015) 101–110.

- [18] L. J. Olson, S. Roy, The economics of controlling a stochastic biological invasion, *American Journal of Agricultural Economics* 84 (2002) 1311–1316.
- [19] S. V. Mehta, R. G. Haight, F. R. Homans, S. Polasky, R. C. Venette, Optimal detection and control strategies for invasive species management, *Ecological Economics* 61 (2007) 237–245.
- [20] C. Sims, D. Finnoff, When is a "wait and see" approach to invasive species justified?, *Resource and Energy Economic* 35 (2013) 235–255.
- [21] B. Leung, D. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, G. Lamberti, An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species, *Proceedings of the Royal Society of London B* 269 (2002) 2407–2413.
- [22] B. Leung, D. Finnoff, J. F. Shogren, D. Lodge, Managing invasive species: Rules of thumb for rapid assessment, *Ecological Economics* 55 (2005) 24–36.
- [23] D. Finnoff, J. F. Shogren, B. Leung, D. Lodge, The importance of bioeconomic feedback in invasive species management, *Ecological Economics* 52 (2005) 367–381.
- [24] D. Finnoff, J. F. Shogren, B. Leung, D. Lodge, Take a risk: Preferring prevention over control of biological invaders, *Ecological Economics* 62 (2007) 216–222.
- [25] R. G. Haight, S. Polasky, Optimal control of an invasive species with imperfect information about the level of infestation, *Resource and Energy Economics* 32 (2010) 519–533.
- [26] J. N. Sanchirico, H. J. Albers, C. Fischer, C. Coleman, Spatial management of invasive species: pathways and policy options, *Environmental Resource Economics* 45 (2010) 517–535.
- [27] C. Perrings, K. Dehnen-Schmutz, J. Touza, M. Williamson, How to manage biological invasions under globalization, *TRENDS in Ecology and Evolution* 20 (2005) 212–215.
- [28] P. Mills, K. Dehnen-Schmutz, B. Ilbery, M. Jeger, G. Jones, R. Little, A. MacLeod, S. Parker, M. Pautasso, S. Pietravalle, D. Maye, Integrating natural

and social science perspectives on plant disease risk, management and policy formulation, *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366 (1573) (2011) 2035–2044.

- [29] C. Perrings, M. Williamson, E. Barbier, D. Delfino, S. Dalmazzone, J. Shogren, P. Simmons, A. Watkinson, Biological invasion risks and the public good: an economic perspective., *Conservation Ecology* 6 (2002) 1.
- [30] K. M. Burnett, Introductions of invasive species: Failure of the weaker link., *Agricultural and Resource Economics Review* 35 (2005) 21–28.
- [31] D. A. Hennessy, Biosecurity incentives, network effects, and entry of a rapidly spreading pest., *Ecological Economics* 68 (2008) 230–239.
- [32] D. Knowler, E. B. Barbier, Importing exotic plants and the risk of invasion: Are market-based instruments adequate?, *Ecological Economics* 52 (2005) 341–354.
- [33] E. B. Barbier, J. Gwatipedza, D. Knowler, S. H. Reichard, The north american horticultural industry and the risk of plant invasion, *Agricultural Economics* 42 (2011) 113–129.
- [34] E. B. Barbier, D. Knowler, J. Gwatipedza, S. H. Reichard, A. R. Hodges, Implementing policies to control invasive plant species, *BioScience* 63 (2013) 132–138.
- [35] J. Touza, A. Pérez-Alonso, M.-L. Chas-Amil, K. Dehnen-Schmutz, Explaining the rank order of invasive plants by stakeholder groups, *Ecological Economics* 105 (2014) 330–341.
- [36] R. D. Horan, E. P. Fenichel, C. A. Wolf, B. M. Gramig, Managing infectious animal disease systems, *Annual Review of Resource Economics* 2 (2010) 101–124.
- [37] R. D. Horan, E. P. Fenichel, Economics and ecology of managing emerging infectious animal diseases, *American Journal of Agricultural Economics* 89 (2007) 1232–1238.
- [38] B. M. Gramig, R. D. Horan, Jointly determined livestock disease dynamics and decentralised economic behaviour, *The Australian Journal of Agricultural and Resource Economics* 55 (2011) 393–410.

- [39] R. Horan, E. P. Fenichel, D. Finnoff, C. A. Wolf, Managing dynamic epidemiological risks through trade., *Journal of Economics Dynamics and Control* (2015) DOI: 10.1016/j.jedc.2015.02.005.
- [40] W. O. Kermack, A. G. McKendrick, A contribution of the mathematical theory of epidemics, *Proceeding of the Royal Society of London A* 115 (1927) 700–721.
- [41] R. Anderson, R. May, *Infectious diseases of humans: dynamics and control*, Oxford University Press, 1991.
- [42] N. F. Britton, *Essential Mathematical Biology*, Springer, 2003.
- [43] L. S. Pontryagin, *Mathematical theory of optimal processes*, CRC Press, 1987.
- [44] A. Mikaberidze, C. Mundt, S. Bonhoeffer, The effect of spatial scales on the reproductive fitness of plant pathogens, arXiv:1410.0587v1 [q-bio.PE] (2014).
- [45] T. Sandler, *Global Collective Action*, Cambridge University Press, 2004.
- [46] J. Touza, C. Perrings, Strategic behavior and the scope for unilateral provision of transboundary ecosystem services that are international environmental public goods, *Strategic Behaviour and Environment* 1 (2011) 89–117.
- [47] R. S. Epanchin-Niell, J. E. Wilen, Individual and cooperative management of invasive species in human mediated landscapes, *American Journal of Agricultural Economics* 97 (2015) 180–198.
- [48] L. J. Olson, S. Roy, On prevention and control of an uncertain biological invasion, *Review of Agricultural Economics* 27 (2005) 491–497.
- [49] C. S. Kim, R. N. Lubowski, J. Lewandrowski, M. E. Eiswerth, Prevention or control: optimal government policies for invasive species management, *Agricultural and Resource Economics Review* 35 (2006) 29–40.
- [50] J. D. Hey, M. S. Patel, Prevention and cure? or: Is an ounce of prevention worth a pound of cure?, *Journal of Health Economics* 2 (1983) 119–138.
- [51] D. A. Hennessy, Prevention and cure efforts both substitute and complement, *Health Economics* 17 (2008) 503–511.

- [52] C. X. Hong, G. W. Moorman, Plant pathogens in irrigation water: Challenges and opportunities, *Critical Reviews in Plant Sciences* 24 (2005) 189–208.
- [53] CABI (Centre for Agriculture and Biosciences International), CABI Invasive Species Compendium: *Solanum lycopersicum* (tomato) datasheet, <http://cabi.org/isc/datasheet/31837>, Accessed: 10th September 2015 (2015).
- [54] K. Themann, S. Werres, R. Lüttmann, H. A. Diener, Observations of *Phytophthora* spp. in water recirculation systems in commercial hardy ornamental nursery stock, *European Journal of Plant Pathology* 108 (2002) 337–343.
- [55] C. M. Brasier, The biosecurity threat to the uk and global environment from international trade in plants, *Plant Pathology* 57 (2008) 792–808.