UNIVERSITY of York

This is a repository copy of Modelling the Impact and Control of an Infectious Disease in a Plant Nursery with Infected Plant Material Inputs.

White Rose Research Online URL for this paper: <u>https://eprints.whiterose.ac.uk/99831/</u>

Version: Accepted Version

Article:

Bate, Andrew Matthew, Jones, Glyn, MacLeod, Alan et al. (5 more authors) (2016) Modelling the Impact and Control of an Infectious Disease in a Plant Nursery with Infected Plant Material Inputs. Ecological Modelling. pp. 27-43. ISSN 0304-3800

https://doi.org/10.1016/j.ecolmodel.2016.04.013

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk https://eprints.whiterose.ac.uk/

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

^aEnvironment Department, University of York, Heslington, York. UK

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

^cDepartment of Computing Science and Mathematics, University of Stirling, Stirling. UK

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

^eDepartment 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

Increases in the movement of people and traded goods as a consequence of globalisation have led to growing concerns about the threat posed by invasive species. 3 especially invasive pathogens of humans, plants and animals [e.g. 1–5]. Recent disease outbreaks in plants, such as the Chalara fungus (Hymenoscyphus pseudoalbidus) affecting ash trees across Europe [6] and the oomycete Phytophthora ramorum affecting many plants including larch in Europe [7] and oaks in the US [8], have focused attention on the policy options to reduce the risks of similar plant disase 8 outbreaks occurring in the future, and the management options to reduce damage g from newly established pathogen populations. These disease outbreaks have also 10 raised concerns about patterns of plant trade, which has been identified as a key 11 introduction pathway for invasive pathogens [9], and on the need for a more prominent 12 role of the private sector in biosecurity practices to mitigate existing risk [10]. 13 Understanding the economic impacts of damage and mitigation is essential for determining optimal policy and management options for invasive pathogens [11]. 15 The body of the literature that combines invasion ecology with economic analysis 16 to deal with these issues has drastically increased in the last decade (for an overview 17 see [12, 13]). Bioeconomic studies explore the management problem from a central 18 authority perspective, focusing on the potential social welfare benefits from policy 19 intervention to limit the risk of invasive species damages using instruments that 20 include port inspections, quarantine and import tariffs [14, 15], import risk screening 21 programs [16, 17], the use of public funds to detect, eradicate and/or control 22 established invaders, and habitat restoration [e.g. 18-20]. Other studies have 23 examined the trade-off between preventive measures before the arrival and control 24 measures after the invader is known to be in the country in order to determine the 25 optimal allocation of limited public resources between these two strategies [e.g. 26 21–26] Here we add to this literature by adopting a private sector perspective, in order 27 to understand the biosecurity vulnerability and management incentives affecting 28 individual businesses. 29

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

 $\mathbf{2}$

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

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

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

3

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

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

78 2. Model derivation

79 2.1. Disease dynamics

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

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

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×output. Consequently, the only real difference would be that different output rates would lead to a more complex replacement term.

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

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

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

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

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

$$dI$$
(2)

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

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

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

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

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

where $\hat{u}_{rem} = u_{rem}\delta^{-1}$, the removal effort per plant generation (which is bounded above by $\hat{u}_{remmax} = u_{remmax}\delta^{-1}$), and $R_0 = \beta N \delta^{-1}$, the basic reproductive number, the expected number of secondary infections from a single infected plant over the lifespan of the infected plant in the nursery in an otherwise wholly susceptible plant stock. The basic reproductive number is fundamental to whether a disease will spread
and is discussed in the results section.

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

• $p(u_{ins})$ is a continuously differentiable function of the restriction effort u_{ins} .

• With no restriction of plant inputs $(u_{ins} = 0)$, some proportion of infected plants, a, will enter the nursery, i.e. p(0) = a where $a \in (0, 1]$.

• With any finite restriction effort, some proportion of infected plant will enter the nursery, i.e. $p(u_{ins}) > 0$ for all finite u_{ins} . This means that it is not possible to completely stop infected inputs from arriving no matter how high the level of effort, be it from the difficulty to recognise asypmtomatic infected inputs, or machine and human error.

• For all restriction effort, increasing restriction effort reduces the proportion of infected plant entering the nursery, i.e. $p(u_{ins})$ is a monotonically decreasing function of u_{ins} (equivalently, $\frac{dp}{du_{ins}} \leq 0$ everywhere).

Any function that is (a) continuous, (b) bounded below (by zero in this case) and (c) 141 monotonically decreasing, must converge to some limit as u_{ins} goes to infinity. We 142 denote this limit b, the proportion of inputs that are infected when unlimited 143 restriction effort is used, where $b \in [0, a]$. A simple candidate that satisfies all of these 144 characteristics is $p(u_{ins}) = (a - b) \exp(-du_{ins}) + b$, is plotted in Fig 2 for various 145 values of d, where d can be interpreted as the effort-effectiveness of the restriction 146 measures, i.e. the reduction in the proportion of infected plant inputs per unit of 14 restriction effort. 148

149 2.2. Bioeconomic model

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



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

and P_I representing the unit net price of those outputs, respectively³. We assume that 153 $P_I < P_S$ since the infection would likely decrease the plants value when mature and 154 could incur higher production costs⁴. The dynamics of the proportion of infected 155 plants within the nursery is given by equation (5). In addition, we assume that disease 156 symptoms become more apparent as infected plants mature. This, together with an 157 assumption of a regime of inspections within the nursery (inspection regime is 158 independent of the state of the nursery, i.e. a constant cost and thus can be ignored), 159 leads to the nursery owner having good knowledge of which plants are infected and so 160 can act accordingly if desired. All the mature plants sold, or those subject to removal 16 control, are immediately replaced given a constant price P_{in} of plant inputs. This is 162 consistent with our earlier assumption of constant stock within the nursery. 163 We also consider the costs of removing infected plants and undertaking restrictions 164 measures to prevent buying infected input plant material. The cost of removing 165 infected plants should increase both with the number of infected plants and with the 166 removing control effort, u_{rem} . Consequently, we will assume for simplicity that the 167 cost of removing infected plant is linearly dependent on the number of infected plants 168 and to prevent the unfeasible case of unbounded removal control effort, we will set a 169 maximal value of removal control effort of u_{remmax} . Similarly, the cost of the 170

 $^{^3 \}rm We$ 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.

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

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

$$\max_{u_{ins}, u_{rem}} \operatorname{Profit} = \int_{0}^{T} \underbrace{e^{-rt}}_{P_{in}(\delta N + u_{rem}I)} \begin{pmatrix} \operatorname{Revenue from selling S} & \operatorname{Revenue from selling I} \\ P_{S}\delta S & + & P_{I}\delta I \\ + & P_{I}\delta I \end{pmatrix} (6)$$

178

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

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

$$\max_{\hat{u}_{ins}, \hat{u}_{rem}} P_S(1-i) + P_I i - P_{in}(1+\hat{u}_{rem}i) - c_{rem}\hat{u}_{rem}i - \hat{u}_{ins}$$
(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 $\hat{u}_{ins} = c_{ins}u_{ins}(\delta N)^{-1}$).

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

 $\hat{p}(\hat{u}_{ins}) = (a-b)\exp(-\hat{d}\hat{u}_{ins}) + b$ where $\hat{d} = d\delta N c_{ins}^{-1}$ such that $\hat{p}(\hat{u}_{ins}) = p(u_{ins})$. Here \hat{d} represents the cost-effectiveness of restriction efforts, i.e. the reduction in the proportion of infected inputs per dollar invested in restricting measures.

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

$$\max_{\hat{u}_{ins},\hat{u}_{rem}} \left(\overbrace{P_I - P_S}^{\text{revenue lost from infecteds}} - \overbrace{(P_{in} + c_{rem})\hat{u}_{rem}}^{\text{restriction costs}} \right) i - \overbrace{\hat{u}_{ins}}^{\text{restriction costs}}$$
(8)

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

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

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

216 subject to

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

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

218 2.3. Analysis

We start the analysis of the system (9)-(10) by looking at the long term disease 219 dynamics for a given constant control regime. We compare the case where restriction 220 is perfect, i.e. all plant inputs are susceptible $(p(u_{ins}) = 0)$ with a case where 221 restriction is imperfect, i.e. some plant inputs are infected $(p(u_{ins}) > 0)$. Following 222 this, we derive the necessary conditions describing optimal level of effort in restriction 223 and removal strategies, using the equilibrium found in the imperfect restriction section. 224 Subsequently, we demonstrate some of the theoretical results with numerical solutions. 225 For simplicity, we will focus on exploring how the optimal level of management 226 changes with respect to changes in key parameters: the basic reproductive number 227 (R_0) , the loss in revenue from selling an infected mature plant (L) and the 228 cost-effectiveness (d) (the decay in the proportion of infected plant inputs per dollar 22 spent in restriction efforts) and keep all other parameters fixed. This means, as a 230 baseline, we assume that (i) the background level of infection within the input plant 231 material is a = 0.2, so the disease is widespread within the traded plant material; (ii) 232 it is possible to restrict all infected inputs with unlimited restriction b = 0, and *(iii)* 233 the cost of removing and replacing an infected is set at C = 10. The nursery's 234 maximum level of effort on removal is assumed to take any value up to $u_{remmax} = 6$. 235 For the basic reproductive number, we will consider two cases, $R_0 = 0.5$ (i.e. the 236 disease cannot spread within the nursery, Scenario 1) and $R_0 = 5$ (i.e. the disease 237 spreads fast within the nursery, Scenario 2). Although the value of R_0 will depend on 238 the characteristics of the particular disease and the plant, given that established 239 human diseases can have values up to the mid teens (measles has a value of 240 $R_0 = 12 - 18$) and that many human diseases have basic reproductive numbers in the 241 realms of 5 [41], values of R_0 have rarely been found in plants diseases. Even though, 242 one study has found that R_0 is of the order of 50 for wheat stripe rust in large wheat 243 fields [44]. Moreover, the values of R_0 is a factor that depends not only on disease 244 traits, but also on the properties of the nursery. For example, actions like the routine 245

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.

For the loss of revenue from selling an infected plant, we consider a value of L = 10250 as our baseline, which implies that the costs of removal are the same as the losses made 251 from selling an infected plant; this would be compared to scenarios with smaller values 252 for L, in particular, in Scenario 1b, L = 5 and in Scenario 2b, L = 1. It is reasonable 253 to assume that smaller values of L would correspond to situations where the diseased 254 plants have superficial damage and/or there are secondary markets for infected plant 255 outputs with little difference in the net price of healthy mature plants. Higher values 256 of L correspond to disease that have a large impact on the net price of a highly 257 valuable plant, without an effective secondary market for infected plants. In particular, 258 plants with that take a long time to mature or bespoke plants sold to the landscape 25 sector tend to sell for higher prices and thus prone to large losses from infection. 26

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

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

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			

Table 1. The Scenarios and their key results

Here, $\stackrel{i}{\downarrow} p'$ 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 $(p(u_{ins}) = 0)$

In the absence of the removal of infected plants (i.e. $u_{rem} = 0$), we have two cases: 281 (1) $R_0 < 1$: In this case, on average, a single infected plant infects less than one 282 susceptible plant over the lifetime of the infected plant and hence the disease will die 283 out eventually. Consequently, the only stable state is the disease-free state and thus 284 the disease cannot become endemic $(i^* = 0)$ (Fig 3(b)). (2) $R_0 > 1$: Here, a single 28 infected plant infects more than one susceptible over the lifetime of the infection and 28 hence the disease will spread out from any single introduction. Hence, the only stable 28 steady state is the endemic steady state $i^* = 1 - \frac{1}{R_0}$ and thus any introduction will 288 result in the disease being endemic (Fig 3(a)). 289

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

endemic from any single introduction (Fig 3(b)).

Now, for $u_{rem} > 0$, we have that $R_0^{rem} < R_0$. Thus, the disease will find it harder 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 $u_{rem} = 0$, $R_0^{rem} = R_0$.

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

301 3.1.2. Imperfect restriction $(p(u_{ins}) = p > 0)$

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

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

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

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



Figure 4. Imperfect restriction $(\mathbf{p} > \mathbf{0})$ (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.

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

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

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

Working with the prevalence steady state, we seek to find the optimal combination of removal and restriction, u_{rem} and u_{ins} that minimises the costs of the plant disease 330 at the nursery:

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

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

$$\frac{\partial Q}{\partial u_{rem}} = \mathrm{MC}_{rem} - \mathrm{MB}_{rem} = 0 \tag{13}$$

$$\frac{\partial Q}{\partial u_{ins}} = \mathrm{MC}_{ins} - \mathrm{MB}_{ins} = 0 \tag{14}$$

where

$$\begin{split} \text{MB}_{rem} &= \frac{(L + Cu_{rem})(1 - p(u_{ins}))}{2R_0} \left(1 + \frac{M}{\sqrt{M^2 + 4R_0 p(u_{ins})}}\right) \\ \text{MC}_{rem} &= \frac{C}{2R_0} \left(M + \sqrt{M^2 + 4R_0 p(u_{ins})}\right) \\ \text{MB}_{ins} &= -\frac{(L + Cu_{rem})\frac{\partial p(u_{ins})}{\partial u_{ins}}}{2R_0} \left(u_{rem} + \frac{Mu_{rem} + 2R_0}{\sqrt{M^2 + 4R_0 p(u_{ins})}}\right) \\ \text{MC}_{ins} &= 1 \end{split}$$

As expected, Equation (13) (Equation (14)) requires a nursery owner to allocate resources to removal (restriction) until the last dollar spent on removal (restriction) equals the marginal benefits gained in terms of reduction in infection costs. The analysis of the properties of local and global minima for removal (Equation (13)) and restriction (Equation (14)), can be found in Appendices A and B, respectively. Looking at Equations (13) and (14) and incorporating the results found in Appendices A and B, we have the following:

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

• If $MB_{rem} < MC_{rem}$ at $u_{rem} = u_{remmax}$ then $MB_{rem} < MC_{rem}$ for all admissible u_{rem} and thus $u_{rem} = 0$, i.e. no removal effort, is the global minimum with 345 respect to u_{rem} . 346 • The only other case with respect to u_{rem} is that there exists a value of 347 $u_{rem} \in (0, u_{remmax})$ such that $MB_{rem} = MC_{rem}$, and this internal solution is a 348 local maximum. Both $u_{rem} = 0$ and $u_{rem} = u_{remmax}$ are local minima with 349 respect to u_{rem} . One of these will be the global minimum with respect to u_{rem} 350 and direct comparison of the values of Q at these local minima is required. 351 • With respect to restriction, if $MB_{ins} < MC_{ins}$ at $u_{ins} = 0$, then $MB_{ins} < MC_{ins}$ 352 for all $u_{ins} > 0$ and thus Q is minimised at $u_{ins} = 0$, i.e. no restriction is optimal. 353 • Conversely, if $MB_{ins} > MC_{ins}$ for $u_{ins} = 0$ (for fixed u_{rem}), then there is a value 354 of $u_{ins} > 0$ such that $MB_{ins} = MC_{ins}$ (i.e. a level of restriction where the 355 marginal benefit is equal to the marginal cost), and this value is the global 356 minimum with respect to u_{ins} , i.e. moderate restriction is optimal. 357 • One can analyse whether removal and restriction work together as complements 358 or as substitutes by analysing $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}}$. For complements, $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} < 0$ 359 (since Q represents costs, not profit or utility) and $\frac{\partial^2 Q}{\partial u_{ins}\partial u_{rem}} > 0$ for substitutes. 360 The expression for $\frac{\partial^2 Q}{\partial u_{ins}\partial u_{rem}}$ is complex and can be either sign. In particular, if 361 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 362 and removal are complements; whereas, if u_{rem} is large and thus M is large and negative, $\frac{\partial^2 Q}{\partial u_{ins} \partial u_{rem}} > 0$, making restriction and removal substitutes. 364 From this and by looking at Equations (13) and (14), we can establish some rules 365 of thumb. Firstly, by looking at Equation (14), we can see that increasing L and/or C, will increase the marginal benefits in damages avoided and thus generally results in 36 higher restriction (in particular, it never leads to lower levels of restriction). Secondly, 368 looking at Equation (13), we can see that increasing L and C proportionally results in 369 no change in whether $u_{rem} = 0$ or $u_{rem} = u_{remmax}$ are optimal. Consequently, the 370 values of L and C themselves have no impact on the optimal strategy for removal, only 371

344

the ratio between L and C (in other words, the nursery owner would apply the same 372

effort if losses for an infected plant were \$1 and removal costs \$1 as \$10 losses with \$10 373

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.

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

of $\frac{\partial p(u_{ins})}{\partial u_{ins}}$ in MB_{ins} suggests that increasing the cost-effectiveness of restriction, d,

increases MB_{ins} around $u_{ins} = 0$, making restriction measures more likely.

380 3.3. Optimal management: Numerical solutions

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

382 3.3.1. Scenario 1: Low infectiousness

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

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

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

Next, we consider the case where the revenue losses from infection are considerably lower (Scenario 1b, Fig 5(b)). Reducing the revenue losses from infection from L = 10to 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.

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
- 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
- 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)).

3.3.2. Scenario 2: High infectiousness 414

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

When a disease is highly infectious, any small introduction of infected plants will 417 spread the disease through the nursery quickly. Consequently, investing in restriction 418 does not prevent the disease going through the plants growing in the nursery. 419

However, restriction does have a mild effect on disease prevalence when prevalence in 420 the nursery is high as the 'cleaner' inputted plants that replace those leaving the 421 nursery will have a mild rinsing effect. Thus, without removal effort, restriction is 422 often not viable (i.e. no restriction is optimal) when the disease is highly infectious.

This is particularly the case here when contrasting the viable restriction in Scenario 1a 424 (Fig 5(a) where $R_0 = 0.5$) and the inviable restriction in Scenario 2a (Fig 6(a)) when 425

there is no removal. 426

42

In Scenario 2a (Fig 6(a)) there are up to two local minima. We know from the 427 analytical results that optimal removal is either $u_{rem} = 0$ or $u_{rem} = u_{remmax}$. 428 Consequently we can argue about the importance of u_{remmax} by varying 429 $u_{rem} = u_{remmax}$ in the contour plots, following the $MB_{ins} = MC_{ins}$ line. If the nursery 430 capacity to remove is small, in particular such that u_{remmax} is below the intersection 431 of the $MB_{ins}=MC_{ins}$ and $MB_{rem}=MC_{rem}$ curves, then there is only one local (and 432 thus global) minimum, which is to do nothing and let the disease take its course. If 433 u_{remmax} is beyond the intersection, then there are two local minima, the 434 aforementioned 'do nothing' and $u_{rem} = u_{remmax}$ with the corresponding restriction 435 level given by $MB_{ins} = MC_{ins}$. The global minimum is one of these two local minima 436 and which one depends on the value of u_{remmax} ; if u_{remmax} is small enough that the 437 contour is either blue or green (below $u_{remmax} \approx 3.5$) then 'do nothing' is optimal, 438 whereas beyond $u_{remmax} \approx 3.5$ where the contours are yellow to red, then maximum 439 removal $(u_{rem} = u_{remmax})$ is the optimal strategy. Consequently, there is a great 440 range of values u_{remmax} where the optimal solution is to 'do nothing', that it is futile 441 to try and control the disease without being able to really get on top of it. 442 One particularly interesting result in Scenario 2a (Fig 6(a)) is the kink that occurs 443

in the $MB_{ins} = MC_{ins}$ curve. This kink occurs indistinguishably close to $R_0^p = 1$ since 444 the kink occurs around where the $MB_{ins}=MC_{ins}$ and $R_0^p = 1$ curves intersect. Below 445



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.

this kink, we have that increasing level of removal is linked with increasing level of 446 restriction, i.e. removal and restrictions are complements. This occurs since restriction 447 improves the effectiveness of removal as it reduces the chances that an infected plant, 448 which has been removed, is replaced by another infected plant. However, above the 449 kink, we have that increasing level of removal results in a decrease in the optimal level 450 of restriction, i.e. they are substitutes. This agrees with the final bullet point of 451 the analytical results, where restriction and removal are complements 452 when R_0 is large and u_{rem} is small, whereas restriction and removal are 453 substitutes when u_{rem} is substantially larger than R_0 . 454 Going from Scenario 2a to 2b (Fig 6(b)), there is a reduction in the loss in revenue 455

from selling an infected plant from L = 10 to L = 1 (note that this is a considerably smaller revenue loss than in Scenario 1b). The effect of this small revenue loss in the

optimal effort of controlling the disease is relatively minor with respect to Scenario 2a; 458 $MB_{ins}=MC_{ins}$ has shifted a little to the left, and thus the optimal level of restriction 459 is reduced everywhere and $MB_{rem}=MC_{rem}$ has shifted a bit to the right and a little 460 up. The consequence of the move in $MB_{rem} = MC_{rem}$ is that removal is also less viable 461 everywhere. In particular, the intersection between these two lines that separates the 462 two local minima has shifted up, increasing the region where there is only one local 463 minimum; and consequently, 'do nothing' has become the optimal control irrespective 46 to the value of u_{remmax} . 465

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

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

490 4. Discussion and Conclusions

In this paper, we have analysed the prevention and control management options 491 available to a nursery owner in order to minimise the impacts of an infectious disease 492 that may spread within the nursery. To this end, we derived a bioeconomic model of a 493 plant nursery, where the manager can opt either to restrict the proportion of infected 494 plant material coming into the nursery (prevention), or remove infected plants within 495 the nursery (control), or a combination of both strategies. We assume that there is an 496 upper limit on removal effort. Our analytical results show that (a) if infected inputs 497 are always coming into the nursery, the disease would persist in the nursery, and will 498 approach a unique endemic steady state (Section 3.1.2 and Figure 4); (b) the optimal 490 removal is either maximum removal (i.e. the upper limit in removal efforts given the 500 nursery's capacity) or no removal, as long as restriction efforts are optimally allocated, 50 i.e. where the marginal cost of restriction equals its marginal benefit in terms of 502 disease damages avoided (Section 3.2); (c) optimal restriction expenditure increase 50 with both the revenue losses for selling mature infected plants and costs of removal; 504 while maximal removal is more likely to be optimal if either revenue infection losses 505 increase or removal costs decrease (Section 3.2); (d) since any removed infected plant 506 stock needs to be replaced buying new plant inputs, which could potentially be 507 infected, the manager can increase the effectiveness of removal effort by increasing 508 restriction effort (see expressions of R_0^p and i^* in Section 3.1.2). 509

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

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

23

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

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

This phenomenon where 'prevention' and 'cure' are complementary has been found 553 in the human health literature in [50, 51]. Hennessy et al. [51] argue that for 554 'prevention' and 'cure' being complements is that increasing prevention reduces the 555 chance that cured individuals become sick again and thus improving the long term 55 benefit of curing sick individuals. This argument is analogous to the reasons that can 55 explain why restriction improves the effectiveness of removal in Scenario 2, as the 558 replacement of a removed infected plant with an infected plant can be seen as 559 (instantaneous) reinfection. 560

We also show that this complementary relationship between prevention and control 561 continues as removal level increase until around $R_0^p = 1$. Beyond this point the disease 562 no longer is able to spread through the nursery and instead relies on the constant 563 introduction of infected plant inputs to persist in the nursery. In this case, the disease 564 could be manageable through the removal programme, and the nursery owner can 565 choose whether to remove it once it is in the nursery or prevent it from entering the 56 nursery. This means, restriction and removal efforts are substitutes, akin to the classic 56 'prevention vs cure' argument. 568

However, it should be noted that the analysis in this paper is based on the long 569 term dynamics of the disease and decision making, thus our work fits more the 570 endemic stage of an infection with the nursery being subject to continual invasion 571 pressure. Consequently, it neglects the epidemic/invasion stage, and uncertain benefits 572 from delaying the spread of the disease through prevention and/or survelliance during 573 this stage [e.g. 19, 25]. Moreover, we also recognise that many nurseries work on a 574 shorter term basis than used in this model. For example, some nurseries are seasonal 575 and only have a generation or two of plants in the nursery for one season before an 576 annual reset of the nursery, with new plants stock. In this case, a steady state might 57 not be appropriate analysis as not enough time has occurred for a steady state to be 578 reached. Following the above literature, in cases like those in Scenario 2 with highly 579 infectious diseases, restriction and removal may be more viable in the early stages of 580 disease introduction (unlike the long term) since they can delay the inevitable disease 581 spreading through the nursery. However, even in shorter time-scales, 582

equilibrium-based analysis form a strong baseline for understanding optimal decisions.

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

⁵⁸⁵ nursery is always full). This is not always true, especially if seasonal effects (like ⁵⁸⁶ weather or seasonal demand) occur or if the nursery owner reduces the size of the ⁵⁸⁷ nursery as a disease management tool. During periods with a reduced nursery stock, ⁵⁸⁸ the basic reproductive number R_0 is reduced (since the disease is density dependent) ⁵⁸⁹ as is the cost-effectiveness of restriction, 'd'. The reduction in R_0 means the disease ⁵⁹⁰ 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 591 limit to the extent of the disease will spread and thus a worst case scenario in terms of 592 uncontrolled damages from a pathogen. On top of that, the reduction on R_0 from a 593 lower N reduces the range of u_{rem} where restriction and removal are complements. On 594 the other hand, the reduction in the cost-effectiveness of restriction would result in a 595 less stringent restriction regime (i.e. an increase in the proportion of infected plant 596 inputs, $p(u_{ins})$), akin to what is found when comparing Scenarios 1a and 2a with 597 Scenarios 1c and 2c. 59

In this paper, we have assumed the disease is an SI disease, i.e. each plant is either 59 susceptible or infected and there is no recovery from the disease. This was for 600 simplicity and generality. However, many plant diseases have recovery, latency, 601 asymptomatic infection and immunity, as well as free-living stages in the environment 602 (i.e. in the soil or water). The presence of asymptomatic and latent infected plant 603 inputs undermines the owner's ability to restrict infected inputs coming into the 604 nursery since identifying infected plants material inputs becomes much more complex 605 or even impossible if no symptoms of infection or clear evidence of pathogens are 606 present. In addition, our analysis only focuses on diseases that can only enter the 60 nursery via infected plant material inputs (i.e. though plant trade). However, for 608 many different nurseries, pathogens and pests get into the nursery through a number 60 of different pathways. In particular, contaminated water is often the reason for 610 Phytophthora and other pathogens getting into plant nurseries [52, and references 611 therein]. We suspect that in this situation, restriction strategies that focus on 612 inspecting plant inputs would have a limited effect on preventing the diseases, which 613 would reduce their cost-effectiveness and therefore their optimal level of provision. 614 The level of restriction in this paper depends greatly on the choice of the function 615 $p(u_{ins})$, the proportion of infected plant material inputs that are infected for a given 616

26

level of restriction. In this paper, we used an exponentially decreasing function to 617 obtain numerical results since it was the simplest function that satisfies the desired 618 properties of $p(u_{ins})$ (i.e. which, in short, is monotonic decreasing of u_{ins}). This 619 function has the property that the first dollar spent on restriction is always the most 620 effective, and that each dollar spent has a smaller effect on $p(u_{ins})$ than the previous 62 dollar. This property would not necessarily be appropriate in several cases. For 622 example, functions where a small investment in restriction has little effect and a 623 substantial investment that more has to spent for a restriction regime to start to have 624 a noticeable effect on the proportion of infected plant materials coming in could be 625 more appropriate if substantial funds are needed for effective levels of knowledge, 626 labour, machinery and skills to be maintained. A suggested simple function that could 627 provide useful incite into management satisfies this property is $(a - b) \exp^{-du_{ins}^2} + b$ (in 628 which case the most cost-effective level of restriction is at $u_{ins} = (2d)^{-1/2}$. 629

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

Acknowledgments

This work was funded by NSF grant 1414374 as part of the joint NSF-NIH-USDA Ecology and Evolution of Infectious Diseases program, and by UK Biotechnology and Biological Sciences Research Council grant BB/M008894/1. The authors would like to thank the anonymous reviewers for their helpful and constructive comments.

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:

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

Consequently, solutions of $\frac{\partial Q}{\partial u_{rem}} = 0$ are solutions of $\left(\left(\frac{L}{C} + u_{rem}\right)(1 - p(u_{ins})) - M\right)\left(\sqrt{M^2 + 4R_0p(u_{ins})} + M\right) - 4R_0p(u_{ins}) = 0$. 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.

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

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

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

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

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 $M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})}$ has its
minimum. So we look at the properties of solutions of
 $\frac{\partial}{\partial M} \left(M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})} \right) = 0.$
 $\frac{\partial}{\partial M} \left(M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})} \right) = 2M + \sqrt{M^2 + 4R_0p(u_{ins})} + \frac{M^2}{\sqrt{M^2 + 4R_0p(u_{ins})}}$
(A.10)
 $= \frac{2}{\sqrt{M^2 + 4R_0p(u_{ins})}} \left(M^2 + 2R_0p(u_{ins}) + M\sqrt{M^2 + 4R_0p(u_{ins})} \right) = 0$ (A.11)

 $= \frac{1}{\sqrt{M^2 + 4R_0 p(u_{ins})}} \left(M^2 + 2R_0 p(u_{ins}) + M\sqrt{M^2 + 4R_0 p(u_{ins})} \right) = 0$ Solutions of this satisfy $M = -\frac{M^2 + 2R_0 p(u_{ins})}{\sqrt{M^2 + 4R_0 p(u_{ins})}}$. Substituting this into $M^{2} + 2R_{0}p(u_{ins}) + M\sqrt{M^{2} + 4R_{0}p(u_{ins})}$ gives:

$$-\frac{M^{2} + 2R_{0}p(u_{ins})}{\sqrt{M^{2} + 4R_{0}p(u_{ins})}} \left(-\frac{M^{2} + 2R_{0}p(u_{ins})}{\sqrt{M^{2} + 4R_{0}p(u_{ins})}} + \sqrt{M^{2} + 4R_{0}p(u_{ins})}\right) + 2R_{0}p(u_{ins})$$

$$= -\frac{M^{2} + 2R_{0}p(u_{ins})}{M^{2} + 4R_{0}p(u_{ins})} \left(-(M^{2} + 2R_{0}p(u_{ins})) + M^{2} + 4R_{0}p(u_{ins})\right) + 2R_{0}p(u_{ins})$$

$$= 2R_{0}p(u_{ins}) \left(1 - \frac{M^{2} + 2R_{0}p(u_{ins})}{M^{2} + 4R_{0}p(u_{ins})}\right) > 0$$
(A.12)

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:

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

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

$$=\frac{\partial^{2} p(u_{ins})}{\partial u_{ins}^{2}} \frac{L+Cu_{rem}}{2R_{0}} \left(u_{rem} + \frac{(Mu_{rem} + 2R_{0})(M^{2} + 4R_{0}p(u_{ins})) - 2R_{0} \frac{\left(\frac{\partial p}{\partial u_{ins}}\right)^{2}}{\frac{\partial^{2} p}{\partial u_{ins}^{2}}} (Mu_{rem} + 2R_{0})}{(M^{2} + 4R_{0}p(u_{ins}))^{\frac{3}{2}}} \right)$$
(B.3)
$$\left(u_{rem} + \frac{M^{2}_{2} + 4R_{0}p(u_{ins}) - 2R_{0} \frac{\left(\frac{\partial p}{\partial u_{ins}}\right)^{2}}{\frac{\partial u_{ins}}{\partial u_{ins}^{2}}} \right)$$

$$=\frac{\partial^{2} p(u_{ins})}{\partial u_{ins}^{2}} \frac{L+Cu_{rem}}{2R_{0}} \left(u_{rem} + \frac{M^{2} + 4R_{0}p(u_{ins}) - 2R_{0} \frac{\left(\frac{\partial p}{\partial u_{ins}}\right)^{2}}{\frac{\partial^{2} p}{\partial u_{ins}^{2}}}}{M^{2} + 4R_{0}p(u_{ins})} \underbrace{\frac{Mu_{rem} + 2R_{0}}{\sqrt{M^{2} + 4R_{0}p(u_{ins})}}}_{\text{always} > -u_{rem}} \right)$$
(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 $\frac{\partial p}{\partial u_{ins}} = -d(a - b) \exp(-du_{ins}) = -d(p(u_{ins}) - b)$ and $\frac{\partial^2 p}{\partial u_{ins}^2} = -d\frac{\partial p}{\partial u_{ins}} = d^2(a - b) \exp(-du_{ins}) = d^2(p(u_{ins}) - b)$. Armed with this, we have:

$$\frac{\partial^2 Q}{\partial u_{ins}^2} = \frac{(L+Cu_{rem})d^2(p(u_{ins})-b)}{2R_0} \left(\underbrace{\underbrace{u_{rem} + \underbrace{\frac{M^2 + 2R_0(p(u_{ins})+b)}{M^2 + 4R_0p(u_{ins})}}_{>0} \underbrace{\frac{Mu_{rem} + 2R_0}{\sqrt{M^2 + 4R_0p(u_{ins})}}}_{>0} \right)$$
(B.5)

$$> 0 \text{ when } L + Cu_{rem} > 0 \tag{B.6}$$

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 $u_{ins} \to \infty$). 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, $\frac{\partial Q}{\partial u_{ins}} \ge 0$ 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:

$$\min_{u_{ins}, u_{rem}} \int_0^{\hat{T}} e^{-\hat{r}t} \left((L + Cu_{rem})i + u_{ins} \right) dt$$
(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:

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

Consequently, the adjoint equation is:

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

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

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

and

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

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:

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

Inserting this into (C.3) gives:

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

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

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

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

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

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

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

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

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

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

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

Substituting this into C.12 and arranging gives

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

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

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

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

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

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

- 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. Liebhhold, 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 hazardsl 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 polices 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-Torrelio, 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.