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The effects of invasive pests and pathogens on strategies for forest diversification

Morag F. Macpherson[a,*], Adam Kleczkowski[a], John R. Healey[b], Christopher P. Quine[c], Nick Hanley[d]

[a] Computing Science and Mathematics, School of Natural Sciences, University of Stirling, Cottrell Building, Stirling FK9 4LA, UK
[b] School of Environment, Natural Resources and Geography, College of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, UK
[c] Forest Research, Northern Research Station, Roslin, Midlothian EH25 9SY UK
[d] School of Geography & Geosciences, Irvine Building, University of St Andrews, North Street, St Andrews, Fife KY16 9AL, UK

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ABSTRACT

Diversification of the tree species composition of production forests is a frequently advocated strategy to increase resilience to pests and pathogens; however, there is a lack of a general framework to analyse the impact of economic and biological conditions on the optimal planting strategy in the presence of tree disease. To meet this need we use a novel bioeconomic model to quantitatively assess the effect of tree disease on the optimal planting proportion of two tree species. We find that diversifying the species composition can reduce the economic loss from disease even when the benefit from the resistant species is small. However, this key result is sensitive to a pathogen's characteristics (probability of arrival, time of arrival, rate of spread of infection) and the losses (damage of the disease to the susceptible species and reduced benefit of planting the resistant species). This study provides an exemplar framework which can be used to help understand the effect of a pathogen on forest management strategies.

1. Introduction

Tree pest and pathogen outbreaks can have negative economic and environmental impacts, especially when large areas of forest are affected (Pimentel et al., 2005; Ayres and Lombardero, 2000). Once a pest or pathogen has established there are relatively few treatments that help diseased trees to recover, therefore any reactive strategy tends to focus on controlling the outbreak (often this is preventing or reducing the spread to other forest areas). On the other hand, anticipatory (proactive) strategies have been proposed to reduce the initial susceptibility of forests to an outbreak, and/or to reduce the impact of disease on the trees once a pest or pathogen has arrived (Quine et al., 2017; Jactel et al., 2005, 2009; Wainhouse, 2004). In this study, a mathematical model is used to examine one such strategy, and in particular to address the question: how does the arrival of a pathogen and occurrence of disease affect the optimal planting strategy with respect to including a second tree species in a mixture?

The literature examining the effect of diversification of the tree species composition of forests on timber and non-timber outputs is ever expanding; however, the range of ecological impacts are difficult to disentangle and explicitly define (Jactel et al., 2009). The type of forest and the objective(s) of the forest owner or social planner will influence the economic and ecological outcomes of diversifying. In this paper, the focus is narrowed by considering a plantation where the manager is interested in the productivity of timber only. Plantation forests are commercially important since they contribute a large proportion of timber to the world markets. They often consist of a single species monoculture chosen for growth or other properties, but are potentially vulnerable to a pest or pathogen of that tree species. For example, over the last century eucalyptus (species of *Eucalyptus* and *Corymbia*) has been grown in non-native plantations in large areas of the southern hemisphere. Their fast growth rate, and separation from their natural enemies has made them an economically important species in South America, South Africa, and more recently South and East Asia (Wingfield et al., 2008). However, the increase in arrival of pests and pathogens, such as cryphonectria canker caused by the fun-

* Corresponding author.
E-mail addresses: mfm@cs.stir.ac.uk (M.F. Macpherson), ak@cs.stir.ac.uk (A. Kleczkowski), j.healey@bangor.ac.uk (J.R. Healey), Chris.Quine@forestry.gsi.gov.uk (C.P. Quine), ndh3@st-andrews.ac.uk (N. Hanley).

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gus *Cryphonectria cubensis* (Wingfield, 2003), is beginning to have a negative affect (Wingfield et al., 2008). Another example is *Ips typographus* that has been shown to have a greater effect on stands with higher proportions of spruce trees (Wermelinger, 2004). Due to the high proportion of *Picea sitchensis* monocultures in the UK, a contingency plan (Forestry Commission, 2015) has been created in case the beetle is found.

With world trade generating a high level of new species invasions (Brasier, 2008), strategies to reduce the impact of pests and pathogens on plantations are of great importance. Species diversification is one such strategy. The main argument for diversifying the tree species composition of production forests is the "insurance hypothesis" since, at the forest level, planting more than one species spreads the risk (Loreau et al., 2001; Pautasso et al., 2005). This means that the initial susceptibility and/or the impact is reduced if a pest or pathogen does arrive, particularly as many are species- or genus-specific in their impact. Modelling in Sweden has shown that there is a reduction in the risk of damage from *Heterobasidion annosum* when *Picea* stands are mixed with *Pinus* (Thor et al., 2005), moreover transmission rates of *Armillaria* spp. were found to reduce with increased tree diversity by Gerlach et al. (1997). Haas et al. (2011) used field data and Bayesian hierarchical models to show that sites with higher species diversity have a reduced disease risk of *Phytophthora ramorum* in California, and the experiments of Hantsch et al. (2014) showed that local tree diversity can decrease the level of fungal pathogen infestations of *Tilia cordata* and *Quercus petraea*. More recently, Guyot et al. (2016) sampled a network of forest plots spanning several countries, and showed a positive relationship between tree species richness and resistance to insect pests. They argued that these "findings confirm the greater potential of mixed forests to face future biotic disturbances in a changing world" (Guyot et al., 2016).

Bioeconomic models can be a useful tool to examine the effect of pests and pathogens on forest management strategies such as species diversification (we provide a short literature review of this research area in Section 2). In this paper, we create a bioeconomic model that finds the optimal planting strategy for two tree species. It is assumed that a forest manager has the option of planting two tree species (species A or species B or both), over a fixed rotation period (note: we consider the effects on optimal rotation for a single species in Macpherson et al., 2016, 2017). We assume that in the absence of a pathogen threat, the commercially preferred species is species A. However, species A is susceptible to a new pathogen that will lower the timber benefit; whereas species B is resistant. The optimal planting strategy, more specifically how much of each species to plant, is the strategy that minimises the expected economic loss.

The mathematical framework for this optimisation problem consists of an objective function that calculates the expected present value loss of planting both species, when compared with the 'ideal situation' of a monoculture of trees of species A remaining un-infected. The potential loss due to planting trees of species A will depend on a number of factors: the probability of arrival of the pathogen and occurrence of disease; when the pathogen arrives within the rotation; how fast the pathogen spreads throughout the forest; and the effect of the disease on the timber benefit (through increased harvesting costs, or reduced growth or reduced quality of the timber). Thus, the objective function depends on the area of infected trees (of species A) at the end of the rotation, which is described by a Susceptible-Infected epidemiological compartmental model.

How fast the pathogen spreads throughout the forest will largely depend on the contact rate (for example, of spores) with a tree, the probability that contact is with a tree of species A, and the probability that the tree is susceptible to disease. This formulation will depend on the spatial arrangement of the trees within the forest, since the probability that contact is made with a tree of species A, will likely be different if species A is planted in a monoculture block, or in an intimate mixture with species B. Whilst we do not explicitly define space in the model, we demonstrate how the pathogen transmission term is constructed for both a monoculture and an intimately mixed forest. Exploring both these cases is important, since the majority of the existing evidence reported above shows a positive effect of tree species diversity (on reducing the effect of disease) when the species in the forest plots are intimately mixed.

The two research questions that this paper addresses are: (1) what is the optimal planting strategy when species A returns a higher timber benefit than species B, but species A is susceptible to a new disease, whereas species B is not, and (2) how do different bioeconomic conditions alter the optimal planting strategy? Examining these questions for a range of bioeconomic parameter sets facilitates a better understanding of the qualitative effects that pathogen characteristics can have on the optimal planting strategy, since our model is not based on a specific host–pathogen system.

The layout of the paper is as follows. A short literature review on using bioeconomic models to analyse the effect of pests and pathogens on forest management strategies is given in Section 2. The economic and epidemiological components of the model are derived in Section 3, and the results are given in Section 4. A discussion in Section 5 is followed by a brief conclusion of the key results found in this paper in Section 6.

2. Bioeconomic modelling of the effect of pests and pathogens on forest management strategies

Changing forest management strategies in response to a pest or pathogen threat often has major economic consequences (Wainhouse, 2004). For example, there will likely be a cost of changing the strategy but, if successful, after a pest or pathogen arrives, the forest output (timber and/or non-timber) may be maintained at a higher level, and thus there will be a benefit (compared with 'doing nothing different'). The decision maker therefore has to weigh-up the costs and benefits of changing the strategy, with the risk of the pest or pathogens arriving, and their predicted effect on the forest.

Mathematical modelling has been used to examine these effects 'in silico'. Models can help to analyse and compare the effect of a pest or pathogen on the relative success of alternative management strategies under different economic and biological conditions. This section highlights some of the bioeconomic models that have been developed to analyse: forest management strategies in the presence of a pest or pathogen; invasion-specific management strategies such as surveillance or control; and the effect of mixed species composition in the presence of other abiotic and biotic risks. (Note that the difference between the first and second cases is that the first assumes that a *change* in a management strategy occurs (i.e. these strategies occur when there is no risk of an incursion), whereas 'invasion specific' strategies are deployed specifically to target management of a pest or pathogen risk.)

There are many forest management strategies whose success may be affected by a pest or pathogen incursion. Jactel et al. (2009) reviewed the effect of a range of forestry practices on biotic and abiotic hazards. Strategies shown to affect the likelihood of an outbreak, and susceptibility of forests to pathogens and pests, included thinning and pruning, tree species composition and density of planting. Using knowledge from practitioners and experts Quine et al. (in preparation) recommended 33 strategies as potentially relevant to combat *Dothistroma septosporum*, in just one country, the UK. Bioeconomic models can be used to explore the effect that disease may have on this multiplicity of alternative strategies, which would be very time consuming to individually test empir-