Invasion landscapes as social-ecological systems: Role of social factors in invasive plant species control

Johanna Yletyinen | George L. W. Perry | Olivia R. Burge | Norman W. H. Mason | Philip Stahlmann-Brown

Abstract
1. Biological invasions are a major threat to biodiversity and human well-being. Scientists and environmental managers typically seek ecological solutions to the biological invasion problem. However, micro-scale social factors, such as landowner attitudes and social interactions that underlie landowners’ willingness to control invasive species, may provide an important lever for controlling biological invasions. Yet, compared to our ecological understanding of invasion dynamics, little is known about the effect of micro-level social factors on the efficiency of invasive species control.

2. Here, we determine how landowners’ micro-scale social factors contribute to the efficiency of invasive species control, that is, landowners’ ability to contain or eradicate invasion at landscape level. First, we survey landowners across New Zealand to gain an understanding of the social factors that affect their willingness and ability to control invasive conifers. Then, we disentangle how micro-scale social factors influence landscape-level patterns of conifer invasion using a social-ecological simulation model. We estimate the influence of social factors individually and through their aggregated effects.

3. We found that micro-scale social factors can determine the efficiency of invasion control to the extent that higher level management strategies, such as early detection of the invasion, become irrelevant. Our experiments support a management strategy for New Zealand conifer invasion that is based on targeting both social and ecological factors. Combining establishment of shared rules for control participation that target socially conditioned behaviour with coordination of control action based on the aggressiveness of the invasion can amplify the efficiency of control at landscape level.

4. Our survey shows that New Zealand landowners are generally highly motivated to control the invasion, but they also adapt their control behaviour to that of others and are limited by the cost of control. The results indicate that integrating such adaptive landowner behaviour with ecological invasion dynamics can, over time, create feedbacks that decrease landowners’ ability to control the invasion.
5. This study demonstrates that failure to consider how social and ecological factors interact in invasion landscapes can lead to suboptimal control programs and irreversible environmental change. A social-ecological perspective on biological invasions will significantly improve our ability to explain and manage invasion dynamics.

**KEYWORDS**
- invasive alien species management
- New Zealand
- plant invasions
- social-ecological models
- social-ecological systems

### 1 | INTRODUCTION

Biological invasions have rapidly increased world-wide, leading to biodiversity loss, ecosystem change and degradation of ecosystem services (Early et al., 2016; Kueffer, 2017; Pyšek et al., 2020; Walsh et al., 2016). Besides their ecological impacts, invasive alien species (IAS) impose financial costs on the agricultural, forestry and fishery sectors (Vilà et al., 2010). The ability of an IAS to spread can be explained to an extent by its ecological traits (Rejmánek & Richardson, 1996) and the characteristics of recipient ecosystems (Blumenthal, 2005); hence, most IAS research and control programs have focused on the ecological characteristics of the invasion. However, controlling IAS in long term or over large spatial extents requires changes in human behaviour (Amel et al., 2017; McLeod et al., 2019). For instance, successful containment of the spread of an IAS often depends on local community members becoming active participants in eradication efforts as well as the ability of an IAS to spread through the landscape (Hobday et al., 2015; Kueffer, 2017). Therefore, failing to consider social complexity or social-ecological dynamics in IAS management could lead to suboptimal IAS control programs and irreversible environmental changes (Bagavathiannan et al., 2019; Epanchin-Niell et al., 2010; Niemiec et al., 2016).

Invasion landscapes are coupled human–environment systems (social-ecological systems, Berkes & Folke, 1998) in which human behaviours and decision-making reciprocally interact with ecological processes. As is characteristic of complex social-ecological systems, the micro-scale processes of invasion landscapes (e.g. property-level control efforts, local species competition) lead to macro-scale patterns (e.g. collective action norms, invasion extent), which, in turn, feedback to the micro-scale processes (Levin et al., 2013). However, compared to our ecological understanding of invasions (Andow et al., 1990; Blumenthal, 2005; Hastings et al., 2005), the human dimensions of biological invasions have received less attention (Shackleton et al., 2019). However, some ecosystems or landscapes may be more vulnerable to biological invasions than others because of the characteristics of the social system to which they are linked. These characteristics could be inherent to the social actors in the system or how they collectively respond to environmental challenges (Yletyinen et al., 2019). For example, the patterns of social interactions between landowners form social network structures that may facilitate or hinder information flows, adoption of new IAS control tools or coordination of collective responses to invasion problem (Bodin, 2017). Another important social aspect of invasion landscapes is actor diversity: differences in landowners’ characteristics, skills, motivations, attitudes and abilities all influence their IAS management capacities (Grêt-Regamey et al., 2019). High actor diversity generally benefits environmental governance, but it can also lead to complicated management situations if landowners differ in their opinion on the need to control the IAS when resources are limited, or struggle to establish common rules for IAS control (Bodin, 2017; Grêt-Regamey et al., 2019). Furthermore, previous research has indicated that the long-term success of IAS control on a property is strongly influenced by action taken on nearby properties (Epanchin-Niell et al., 2010). Without common rules for control, complex social situations may emerge where landowners consider the choices of other local landowners when making IAS control decisions, leading to landowner behaviours becoming interdependent not only through ecological outcomes but also through their influence on decision-making (cf. Ostrom & Ostrom, 2014).

Despite such general knowledge on social factors affecting environmental governance, knowledge of managing social factors associated with IAS—such as leveraging attitudes that underlie landowners’ motivations to participate in IAS control (Cinner, 2018)—remains limited or simplified (Kueffer, 2017; McLeod et al., 2019). The simplification of behaviour may largely result from the *Homo economicus* view that considers human behaviour as perfectly rational, optimised and disciplined in environmental governance, but it can also lead to complicated management situations if landowners differ in their opinion on the need to control IAS (e.g. Niemiec et al., 2017), less is known about how the aggregated effects of landowner behaviours influence IAS control (Bagavathiannan et al., 2019). In large part, these knowledge gaps on both the individual and aggregated effects of social factors on IAS result from a limited understanding of how micro-scale social processes influence the efficiency of landscape-level invasion control (McLeod et al., 2015).
1.1 | Integrated social-ecological approach

We argue that it is crucial to move from considering ecological or social dimensions of IAS control to investigating invaded landscapes as dynamic social-ecological systems, incorporating micro- and macroscale social processes (Levin et al., 2013; Yletyinen et al., 2019). We consider that the invasion and the behaviour of landowners create social-ecological dynamics in which: (a) the IAS spreads, (b) the spread of the IAS influences individual landowners’ responses to invasion, (c) landowners’ decisions to control IAS on their property shape subsequent invasion extent and density and (d) landowners’ decisions affect the behaviour of other landowners, through social influence, and the IAS’s ability to spread to neighbouring properties (Figure 1).

Thus, the success of IAS control emerges from individual, adaptive decision-making alongside context-specific ecological and social contagion processes, and feedbacks between all the three. In this social-ecological setting, we test the hypothesis that micro-level social factors, such as landowners’ individual motivations or social interactions, collectively provide levers for improving the efficiency of IAS control (Niemiec et al., 2016; Schill et al., 2016, 2019). Specifically, we first survey the landowners to gain understanding of the social factors that affect their willingness and ability to control a plant invasion. These social factors include perceptions of the effects of the IAS, landowners’ IAS control behaviour(s) and their interactions with other landowners. Then, we evaluate how individual social factors affect landscape-level IAS control outcomes. To do this in the dynamic social-ecological setting depicted in Figure 1, we use a social-ecological simulation model that combines plant invasion dynamics with landowners’ adaptive decision-making. We consider control efforts ‘efficient’ if the extent and density of the invasion can be contained or the IAS is eradicated from the region. Disentangling the impacts of individual micro-scale social factors on collectively achieved IAS eradication is a first step towards understanding the potential of leveraging social factors in IAS management.

1.2 | New Zealand conifer invasion

Conifer invasion in New Zealand illustrates the social and ecological complexities of biological invasions. Conifers are among the most problematic plant IAS globally (Sapsford et al., 2020). In New Zealand, introduced conifers (including Pinus nigra, Pinus contorta) spread self-sown and unwanted across rural areas (Hulme, 2020). Without rapid action, it is estimated that circa one fifth of New Zealand’s terrestrial area could be invaded by conifers by year 2035, leading to exponential increases in the cost of control (National Wilding Conifer Control Programme, 2014). Invasive conifers directly and indirectly threaten natural landscapes, primary industry productivity, conservation outcomes and residents’ sense of place and culture (Castro-Díez et al., 2019; Gawith et al., 2020; Peltzer, 2018). Humans, however, define the desirability—and, in so doing, management needs—of an IAS through its environmental and socio-economic effects (Head, 2017; Kueffer, 2017; Shackleton et al., 2019). Conifers in New Zealand are social-ecological keystone species (Kueffer, 2017) that have tight interrelationships with economic interests and primary industries. Consequently, controlling conifer invasions in New Zealand is complex because the extent of the invasion requires the involvement of numerous landowners and stakeholders, with different objectives and values associated with invaders and their management (National Wilding Conifer Control Programme, 2014). While many landowners across NZ manage invasive conifers on their properties, and millions of New Zealand dollars (NZD) are annually spent on control programs, conifers in plantation forests (Pinus radiata and Pseudotsuga menziesii) are a valuable economic resource. Forestry is NZ’s third-largest export earner, accounting for NZD 5 billion annually (3% of the country’s gross domestic product) and employing 20,000 people (Forestry New Zealand Te Uru Rakau, 2018; National Wilding Conifer Control Programme, 2014).

Due to their economic value, some landowners may view conifers as beneficial. However, while everyone in effected areas faces the consequences of the conifer spread, few people benefit from...
them (cf. Reichard et al., 2005). From an ecological perspective, hysteresis effects and positive interactions with other introduced species make the conifer invasion challenging to manage (Sapsford et al., 2020; Wood et al., 2015). Conifers are aggressive invaders. They produce significant quantities of viable seed that can spread over long distances by the wind, and the seed may remain viable in the soil for 3 years (Ledgard, 1999). Furthermore, rapid invasion and naturalisation of invasive conifers in New Zealand is driven by interacting environmental and ecological factors (land cover, seed traits, wind, high survival of conifer seedlings etc.; Buckley et al., 2005; Peltzer, 2018).

2 | MATERIALS AND METHODS

2.1 | Study design

We used a survey of New Zealand landowners’ attitudes and behaviours towards a conifer invasion to investigate the social context of the decisions that landowners make about participation in conifer control. We used a simulation model (hereafter, invasion submodel) that represents the spread of the invasive Pinus nigra at a spatial resolution of 1 hectare. We integrated survey data (described below) with the invasion submodel to construct a dynamic social-ecological model that reproduces the spatial pattern of conifer invasion, triggering landowner responses (based on the survey data) in a spatially and temporally realistic manner. Altogether, our Social Ecological Plant Invasion agent-based model (SEPIM) represents 277 rural properties in a circa 870-km² landscape.

Using the SEPIM, we evaluated three management scenarios for on-the-ground control of the conifer invasion: ‘early detection’, ‘early detection failure’ and ‘targeting invasion sources’. Each scenario integrates traditional management factors (advice, funding, early detection) and other micro-level social factors (personal characteristics, views on the impacts of conifer spread, social network influence, influence of neighbour’s actions) as part of landowner decision-making (Table 2). As a control we ran a scenario with no intervention. Using this approach, we evaluated the influence of each social factor on control efficiency in interaction with other social and ecological factors relating to invasion. Thus, our approach allows us to evaluate the outcomes and patterns emerging from social-ecological coupling that independent (i.e. non-coupled) social and ecological models for IAS control are unable to produce. Using these comprehensive survey data, we could capture the effects of social actor heterogeneity on environmental outcomes, an element often overlooked in environmental management programs despite being known to influence management outcomes (Yletyinen et al., 2018).

2.2 | Survey data

The Survey of Rural Decision Makers is a biannual survey launched in 2013 (Brown, 2015) that covers commercial production and lifestyle properties across New Zealand. It gathers information on ownership, landowner objectives, land use, land use change, future planning, social networks, decision support, trust, demographics and risk preferences. The sample of commercial landowners in each Survey of Rural Decision Makers closely approximates the rural population reported in the 2012 nationwide government census of agricultural production by geography, industry and age (Stats NZ Tatauranga Aotearoa, 2020). Since 2015, the Survey of Rural Decision Makers has included questions about invasive conifers, including the presence of conifers in the respondent’s district, attitudes toward conifers and assignments of responsibility for controlling conifers. The survey is largely quantitative, with attitudes measured via Likert-scale questions, and assignments of responsibility, invasion observations etc. assessed via multiple-choice questions.

During winter 2018, 400 respondents from the 2017 Survey of Rural Decision Makers were invited to complete a supplemental survey that focused specifically on invasive conifers, including multiple-choice and open-answer questions detailing accounts of conifer management on own and adjoining land. In total, 277 individuals completed the supplemental conifer survey (hereafter, the survey; Edwards et al., 2020). Detailed survey results are available in Edwards et al. (2020).

The surveys were approved in accordance with the ethical review process of Manaaki Whenua – Landcare Research, within the guidelines of the Code of Ethics developed by the New Zealand Association of Social Science Researchers. This Code of Ethics emphasises informed consent, freedom from coercion to participate, individual privacy, confidentiality and sensitivity to participants’ circumstances. The surveys included a statement of informed consent. It specified that participation is optional, that the respondents can stop answering the survey at any time and that all responses are treated confidentially.

2.3 | Social-ecological Plant Invasion Model: General model concept

The SEPIM consists of: (i) a synthetic landscape divided into properties in which each landowner makes decisions about their participation in conifer control, (ii) landowners and their characteristics and (iii) the landowners’ social connectivity. The landscape is composed of grid cells, each of which holds information on the invasion state (invaded/non-invaded), the density category of the invasion and the time since the cell was invaded. The SEPIM simulates a time period of 30 years. During each annual time step, conifers spread based on the invasion submodel, after which landowners decide whether to control any detected invasion on their property. The probability of detecting conifers on each (invaded) property is determined by a ‘detection probability’ parameter (Table 1); the invasion may, therefore, increase in extent and density undetected for some years, with individuals reaching reproductive age, and therefore not be subject to control until after it has become a new invasion source. If a landowner participates in control efforts, conifers are completely eradicated.
TABLE 1 Factors included in landowners’ adaptive decision-making. The factor influences on decision-making varies from 0 to 1, where 1 indicates a higher likelihood of controlling conifers

| Factor                        | Influence                                                                 |
|-------------------------------|---------------------------------------------------------------------------|
| Social network influence      | This factor models how landowners' control behaviour is influenced by the control behaviour of their contacts (Friedkin, 1998; Granovetter & Soong, 1983), which leads to diffusion of control behaviours through the landowner network. Network connections represent conversations about invasive conifers, which were self-reported in the survey. In practice, social network influence allows control behaviours to spread among landowners. Social network influence \( S \) is calculated as the proportion of links from land users who control conifers of the total number of incoming links. The land user is inclined to make the same choice about control conifers as most of his/her social contacts \( S = \frac{k}{k_0} \) (1) where \( k \) is in-degree (i.e. number of incoming links) from land users who control conifers and \( k_0 \) denotes total in-degree |
| Neighbour influence          | This factor also allows control behaviours to spread among landowners. The effect of neighbours’ actions \( (N_i) \), self-reported in the survey, describes how a landowner would respond if a neighbouring property increased or decreased IAS control. Properties adjoining each landowners’ farm are included in the neighbour influence. Since the model includes binary (control/not control) decision-making, neighbour influence \( (N_c) \) is determined as follows. \( N_c \) denotes neighbouring properties who control conifers, and \( N_{nc} \) those who do not  
  \[ \text{If } \sum N_i > \sum N_{nc} \text{ and } N_c = \text{increase } \rightarrow N = 1 \]  
  that is, land users who have reported they would increase their control behaviour if the control increased in neighbouring properties become more likely to control conifers, where their neighbours increase control 
  \[ \text{If } \sum N_i > \sum N_{nc} \text{ and } N_c = \text{decrease } \rightarrow N = 0 \]  
  that is, land users who have reported they would decrease their control behaviour if the control increased in neighbouring properties become less likely to control conifers, where their neighbours increased control 
  \[ \text{If } \sum N_i < \sum N_{nc} \text{ and } N_c = \text{increase } \rightarrow N = 1 \]  
  that is, land users who have reported they would increase their control behaviour if the control decreased in neighbouring properties become more likely to control conifers, where their neighbours decreased control 
  \[ \text{If } \sum N_i < \sum N_{nc} \text{ and } N_c = \text{decrease } \rightarrow N = 0 \]  
  that is, land users who have reported they would decrease their control behaviour if the control decreased in neighbouring properties become less likely to control conifers, where their neighbours decreased control 
  \[ \text{If } N_i = \text{no change } \rightarrow N = 0.5 \]  
  that is, land users who reported their control behaviour is not affected by that of their neighbours always have their neighbour influence factor set to neutral 0.5 |
| Personal views                | The model includes three survey-based personal view factors: the landowner’s opinion of how invasive conifers have impacted: (i) farm financial performance, (ii) farm environmental performance and (iii) the ease and convenience of management of the property. In the survey, each of these views was estimated on an 11-step categorical scale from 0 = strongly negative to 10 = strongly positive. In the SEPIM, this categorical scale was rescaled to 0 – 1 |
| Personal characteristics      | This factor is based on landowners’ self-reported individual risk preferences \( (R) \) and patience \( (P) \) (see Supporting Information, Table S2 for details on how risk and patience are measured). Its purpose is to provide an approximate estimate of influence of personal dispostion to control (character); in this case, landowners who are unwilling to take unnecessary risk and have patience to control are more likely to participate in control efforts. For this purpose, levels of risk and patience were combined into one factor, personal character \( (C) \), which averages risk-taking and patience: \( C = \frac{R+P}{2} \) (7) |
| Advice                        | A landowner’s need for advice was set to 1 if the survey respondents reported that additional information would be helpful for controlling conifers, and 0 otherwise |
| Funding                       | This factor was based on each survey respondent’s estimate of the difficulty of invasion control on their property, considering both time and financial costs. The difficulty was estimated on an 11-point categorical scale from 0 = ‘extremely easy’ to 10 = ‘extremely difficult’. Funding \( (F) \) is reversed in the model such that an increase in \( F \) indicates increase in favour of control and is scaled to 0–1. \( F \) is then multiplied by the average invasion density \( (d) \) on the landowners’ property to capture increases in cost associated with increased density. \( F = \frac{1}{F_d} \) (8) where 3 is the densest invasion category |
| Background variability        | How much other factors that are not represented in the model can explain decision-making. Noise in the SEPIM was added to each landowner’s control probability as a normally distributed random number with mean = 0.5 and \( \text{SD} = 0.1 \) from that property. During the subsequent time step, invasion proceeds based on the updated invasion area and densities, and control decisions are taken based on updated states of invasion and social influence. State variables capture landscape-level changes in invasion area and density, participation in control and number of years it takes to achieve eradication (where the entire landscape is free of conifers; Supporting Information Table S1). A detailed Overview, Design concepts and Details (ODD) protocol (Grimm et al., 2020) for the SEPIM, a model description customarily for agent-based models, is available in Supporting Information. |
2.4 | Social-ecological Plant Invasion Model: Generation of the landscape

The SEPIM landscape is a grid in which each cell represents two hectares. Invasion dynamics in the SEPIM are aggregated from the 1-hectare (ha) scale of the invasion submodel. We selected 2 ha as an appropriate spatial grain to capture the ecological and the social processes. Using the invasion submodel to calculate input data for invasion dynamics on a 2-ha scale for SEPIM also eases the computation burden of simulating finer spatial grains in the social-ecological model. The landscape is divided into properties of varying sizes. In each property grid, cells are randomly assigned to one of six land covers—high country; hill country (in New Zealand, high country and hill country refer to elevated pastoral land); improved pastures, tussock or unimproved grassland; native bush or shrubland; and river and stream banks—wetlands or coastal areas (Supporting Information Table S3). Based on the patterns of land use in the Canterbury region in South Island, New Zealand, 25% of the landscape is randomly assigned to invasion-resistant covers to capture features that may hinder invasion, such as water bodies and built environments (LAWA Land Air Water Aotearoa, no date; Supporting Information Table S3).

On each time step, each invaded grid cell has one of three invasion categories, based on density: sparse (8–150 conifers/ha), moderate (150–600/ha) and dense (>600/ha). The initial state of the invasion and control are derived from the survey data, that is, landowners’ self-reported awareness of the invasion on their properties and control decision. Properties containing forest plantations are assigned moderate density and are not controlled. This conversion of qualitative survey data to quantitative spatial data may result in mismatches between estimates and exact density measures and distributions of land covers on the properties. For example, landowners’ estimates of what constitutes a dense invasion may vary based on their knowledge on the conifer invasion problem, leading to different observations being categorised under the same density category in the SEPIM. However, we do not believe these mismatches are problematic since we focus on relative changes in invasion area and density to understand social-ecological processes rather than providing explicit invasion forecasts.

2.5 | Invasion submodel

We used Pinus nigra as our model species in the invasion submodel; data for this species are available from Buckley et al. (2005), including seedling establishment, juvenile survival and fecundity. We assigned adult trees to one of the two fecundity rate classes identified by Buckley et al. (2005), based on conspecific competition and the transition probability data they provide. The seed production of P. nigra in New Zealand follows a mast-seeding pattern, with generally low levels of fecundity punctuated by years of extremely high seed production (Coutts et al., 2012). We incorporated mast seeding by simulating inter-annual variation in seed production (see Supporting Information Appendix C: Mast Seeding Simulation). Seed dispersal within 1- hectare ‘sites’ (converted to two hectares scale for SEPIM) followed the processes described in Buckley et al. (2005), while dispersal between sites employed the WALD model (Caplat et al., 2012).

In the SEPIM, invasion follows a chronological process: trees establish, reproduce after maturity (7 years) is reached and then invasion subsequent to reproduction and dispersal occurs. The density of conifers on newly invaded sites depends on their distance from the invasion source and density of existing invasion (Supporting Information Table S4). Infilling is represented in the model: grid cells transition to a higher density class after the nth year of establishment in the cell, as determined by the transition times produced by the invasion submodel (presented in Supporting Information Table S4). After the invasion process, at each time step the subsequent social and ecological dynamics are influenced by the management scenario considered; we describe these scenarios further below. Detailed information on the invasion submodel can be found in the Supporting Information Text ‘Model description for invasion submodel’.

2.6 | Landowner agents and decision-making

In the SEPIM, individual decision-making is based on landowners’ individual characteristics, social influence and the affordability of the control, combinations of which are derived from the survey (Figure 2; Table 1).

Landowners’ individual characteristics consist of a set of landowners’ views and personality traits (Small et al., 2016) self-reported in the 2015 survey and the 2017 conifer-focused surveys, specifically, views on impacts of the conifers, landowners’ time and risk preferences, and need for additional information on invasion control (Table 1). In addition, the SEPIM includes a general cost threshold above which landowners will not participate in control action because it is too expensive. Thus, lack of affordability is the first barrier for participating in invasion control and can override all other factors in decision-making (Table 1; Figure 2). As the influence of affordability is self-evident, we only test it with parameter values 0 (no cost threshold) and 0.1, where the value of 0.1 will result in landowners who find conifer control very difficult, not undertaking control (Table 2). Landowners adjust their perception of the difficulty of controlling conifers on their own property on the basis of the current invasion density.

The SEPIM captures landowner adaptation to other landowners’ control behaviour through social network influence (Friedkin, 1998) and ‘neighbour influence’ (Table 1). Both factors are based on survey data, and the latter describes how survey respondents change control behaviours if neighbouring properties changed their control behaviour. Together, these factors allow control behaviours to spread among landowners. The social network of landowners is based on how many people the respondents self-reported that they had discussed invasive conifers with, both within the region and restricted
FIGURE 2  General logic of landowners’ adaptive decision-making. Decision-making (blue boxes) is part of a social-ecological feedback between invasion dynamics (green) and behavioural responses (yellow). The decision to control invasive conifers (marked in the figure as control or no control) emerges from several factors. Note that most factors influencing decision are not binary (yes/no) in the SEPIM although they are represented here as such for simplicity.

TABLE 2  The four management scenarios. Parameter values represent the weight with which each factor influences decision-making. For example, 0.1 indicates little influence on the decision and 1.0 indicates total influence. Values for detection probability indicate the probability of the detection in the current time step. In the experiments, the weighting for each view was varied separately, as was character, although these factors are included in the same column in the table. In contrast, advice and funding were combined into one factor, and the social network influence and neighbour influence into one.

| Management scenario (experiment)                                | Personal views and character | Social influence | Advice and funding | Detection probability |
|-----------------------------------------------------------------|------------------------------|-----------------|--------------------|-----------------------|
| No control: invasion on the landscape, landowners do not control the invasion | NA                           | NA              | NA                 | NA                    |
| Early detection failure: In the years following invasive conifers control, landowners do not inspect their properties for seedlings that may have been unnoticed in control efforts. Thus, if seedlings have remained on the property, the property becomes invaded without dispersal from an external seed source. To test the influence of early detection failure, the probability for seedlings to remain on land is varied (seedlings probability). Undetected seedlings become detectable to landowners at 3 years’ age | 0.1, 0.5, 1                 | 0.0, 0.5, 1      | 0.0, 0.5, 1          | 0.3, 0.5, 1           |
| Early detection: In the years following conifer control, landowners inspect their properties and remove seedlings that may have survived control efforts | 0.1, 0.5, 1                 | 0.0, 0.5, 1      | 0.0, 5, 1           | 0.3, 0.5, 1           |
| Invasion sources: management targets sources of invasion: (i) unrestricted economic support is provided to landowners (‘target group’) who have invasive conifers in reproductive age (‘target group’), and (ii) forestry plantations do not grow the species that landowners strive to eradicate from the landscape, that is, there is no invasion from forestry plantations | 0.1, 0.5, 1                 | 0.0, 0.5, 1      | Target group: no funding limit, other landowners: 0, 0.5, 1 Advice: 0, 0.5, 1 | 0.3, 0.5, 1 |

To adjoining properties. The social network is binary (all links equally influential). Directed links to adjoining properties were added based on the overall degree distribution as reported in the survey. If a landowner’s neighbour degree (i.e. number of links) was higher than the number of neighbours available in the synthetic landscape, the neighbour degree was the maximum number of neighbours. Links
to landowners on properties elsewhere in the region (regional links) were added by generating undirected random graphs with given degree sequences. Those landowners who reported that they had not spoken to friends or neighbours about conifers were added as isolates, that is, unconnected network actors.

In the SEPIM, each landowner’s probability of participating in control efforts is estimated via a weighted sum model similar to those used in multi-criteria decision analysis. Every factor’s influence is a continuous variable ranging between 0 and 1 or is binarised to 0 or 1. All factors are benefit factors, that is, increases in their value favour participation in control. A landowner’s probability of deciding to engage in control \( P(\text{control}) \) is calculated as the sum of all factors \( i (x_i) \) multiplied by their weights \( w_i \); see Table 1 for factors and Table 2 for weights, i.e. parameter values), divided by the highest possible value (i.e. \( x = 1 \) for each factor).

\[
P(\text{control}) = \frac{\sum_{i=1}^{n} x_i w_i}{\sum_{i=1}^{n} w_i}. \tag{1}
\]

The parameter values (weights) of all factors included in decision-making are rescaled to sum to 1 and analyses are performed on the adjusted values. The adjustment considers the sum of the three view variables as one influence factor. The social influence factor includes both social network and neighbour influence.

To disentangle the effect of each micro-level social factor, we varied the parameter values determining the importance of each factor in decision-making and investigated how increasing the importance of each factor correlates with control efficiency (Table 2). The same approach was taken for the detection probability factor that precedes decision-making, that is, the probability of landowner to notice invasion on their property. We used the weight 0.1 for the external variability factor so it had some influence on the model, but not so much that it would mask the other social and ecological factors. To disentangle the factors leading to efficient control outcomes in our model experiments, we examined correlation (Pearson’s \( r \)) between the micro-scale social factors and control efficiency state variables.

2.7 | Management scenarios

We evaluated the effects of micro-level social factors on control efficiency in the context of three management scenarios (Table 2). Since the effects of micro-scale social factors could differ with management context, we selected three common management scenarios to evaluate social factors. Conifer control is uncoordinated in all scenarios, that is, no collective action or collective rules were in place and landowners participate in control efforts purely voluntarily. First, in the ‘no control experiment’, conifers are allowed to spread in the landscape without landowners controlling them, and this experiment represents our null model. The ‘early detection experiment’ and ‘early detection failure experiment’ test the importance of follow-up inspections in the years after control has taken place on a property. In the absence of inspection, seedlings may lead to reinvasion of the controlled property even in the absence of seed dispersal from beyond the property. The ‘invasion sources experiment’ focuses on targeting sources of invasion—forestry plantations and properties containing conifers of reproductive age.

3 | RESULTS

3.1 | Social context of New Zealand conifer invasion control

The results of our surveys (2017 Supplementary survey focusing on invasive conifers, 277 respondents and 2015 and 2017 Surveys of Rural Decision Makers) show that the majority of landowners control conifers if detected on their property. In 2015, 23% of the respondents considered invasive conifers to be more beneficial than harmful. However, by 2017, only 7% of the respondents considered invasive conifers to be beneficial (Edwards et al., 2020). Nevertheless, most respondents reported that the primary responsibility for controlling conifers lies with government and landowners whose land was the source of invasion; only 22% of respondents \((n = 911)\) believed it to be the responsibility of those landowners whose land has become invaded.

Landowners’ decisions to participate in conifer control efforts are affected by their attitudes towards environmental stewardship, cost of control and actions taken on adjacent properties. The majority of those asked about their control of conifers reported that they control conifers when they were detected on their own property (73 of 94 [78%] respondents). Of these respondents, 33% reported environmental stewardship as the primary reason behind the decision to control conifers. Improving or maintaining pastures was the second most important reason to control conifers (24%), followed by protecting native species and habitats (22%), and restoring native landscapes/views (15%). Most of the respondents considered invasive conifers to have highly negative impacts on the ease of managing their farms and the environmental and financial performance of their farms (Figure 3); on the scale of 0 (strongly negative impact) to 10 (strongly positive impact), most farmers chose one for each type of effect (74% of respondents for financial, 61% for farm management and 55% for environmental impacts, of 89 respondents). The reasons most frequently given for not controlling conifers were that it is too time-consuming or expensive (14 of 24 [58%] respondents) or that reinvasion was inevitable because neighbours did not control invasions (7 of 24 [29%] respondents).

Intriguingly, activities undertaken on neighbouring properties affect landowners’ decisions to control conifers on their own property. Approximately one fifth of the respondents reported that they would decrease their control efforts if neighbours increased their effort (19% of 76 respondents). However, 13% would increase their efforts if neighbours increased their efforts. If neighbouring properties reduced their control efforts, more than one third of
respondents would increase their control efforts (37%). In the same situation, 4% of respondents would decrease their own control efforts. Furthermore, 59% of the survey respondents would increase their control efforts if a new forestry plantation was established on their neighbouring property.

More than half of the respondents considered invasion on their land to be easy to control: 63% of 74 respondents considered control difficulty to be between the levels 0 and 4 on an 11-point scale, where 0 is extremely easy and 10 is extremely difficult. Only 4% of land owners consider it ‘extremely difficult’. Several respondents reported that additional information or advice would help them to control conifers (36% of 201 respondents). More than one third of the respondents had spoken about invasive conifers with their friends or neighbours (37% of 206 respondents).

3.2 | Management factors determining control outcomes

Of the factors we tested (Tables 1 and 2), control efficiency was strongly or moderately correlated with advice and funding, social influence, personal character, views on financial effects of conifers and the extent of baseline invasion (Figure 4). The same five factors correlated with the control efficiency outcomes in all three management scenarios that included control action. However, the strength of correlation of each factor with control efficiency...
outcomes varied across the scenarios (e.g. the correlation between advice and funding and control efficiency; Figure 4). Intriguingly, social influence was negatively correlated with all desirable outcomes, including a strong negative correlation with the maximum number of landowners participating in control ('maximum control') in all three management scenarios. In contrast, increasing the weights of personal character, views on the financial effects and advice and funding in landowner decision-making were all positively correlated with control efficiency outcomes across all management scenarios. All social factors were moderately or strongly correlated with maximum control, but not with all the environmental indicators of control efficiency outcomes.

None of the management factors we tested correlated with the time taken to eradicate conifers from the landscape. However, the number of invasion-free years increased under all management scenarios when control efforts began in the early stage of invasion (low baseline invasion) and social influence had little weighting in the landowner decision-making. The other factors correlating positively with the non-invaded years varied across the management scenarios (Figure 4). The level of baseline invasion correlated only with the number of years when the landscape was not being invaded (non-invaded years), indicating that starting control efforts in the early phase of the invasion resulted in more rapid or more persistent eradication. In contrast to our initial expectations, detection probability and probability of seedlings remaining after control did not correlate with the control efficiency. Finally, we did not vary the affordability parameter much because we expected greater affordability to directly lead to greater control efforts; this was, in fact, the case.

3.3 | Control efficiency

The three management scenarios were equally successful in constraining invasion extent and density (Figure 5). In all the experiments including control action, the invasion extent decreased on average by 20% (SD = 8.9) in comparison to the baseline invasion. Mean density-specific changes under all three management strategies, the mean changes in invasion extent by density category were as follows: 1% decrease in the extent of dense invasion, 11% decrease in moderate and 8% decrease in sparse invasion extent.

In the ‘no control’ experiment (Figure 5), which did not include any conifer control efforts, the mean increase in invasion extent was 19% (SD = 5.5). The experiment also resulted in an increase in

**Figure 5** Experiment-specific changes in invasive conifer densities. The boxplots show changes in the densities of landscape-level conifer invasion from the baseline invasion to the end of simulations. For each experiment, change is captured as a per cent change in the landscape area covered by each category of conifer invasion density. In the ‘no control’ experiment, the area under sparse baseline invasion decreases compared to the initial starting point, while areas with moderate and dense baseline invasions increase. In the other experiments, which include conifer control, areas for sparse and moderate invasions decrease more than dense invasion area, where the median change was close to 0. The horizontal line indicates the median, the bottom and top of the box show the 25th and 75th percentiles; the black dots are outliers.
landscape-level conifer density, including an average 17% increase ($SD = 9.6$) in the extent of dense conifer invasion, 10% increase ($SD = 9.8$) in moderate and 8% decrease ($SD = 7.3$) in sparse invasion.

4 | DISCUSSION

4.1 | Micro-level social factors as levers for IAS control

The scale and pervasiveness of the IAS problem means there is an urgent need for more effective control action (Hulme, 2006). By employing a dynamic social-ecological approach to investigate the role of micro-scale social factors on IAS control efficiency, we have shown that simultaneously considering social and ecological processes in biological invasions reveals new opportunities and challenges for controlling IAS. Our results demonstrate how the aggregated effects of micro-scale social factors can influence IAS control efficiency at the landscape level. First, our survey results regarding the drivers and barriers of control behaviour reveal the complexity of the social dimension of invasion landscapes. While most surveyed rural landowners did not consider conifer control to be the responsibility of affected landowners, the majority nevertheless controlled conifers when they encountered them on their property and identified environmental reasons as their main motivation. Moreover, the effects of invasive conifers were considered severe, but the perceived cost and inevitability of reinvasion made some landowners reluctant to control them. These findings reflect not only the adaptive and complex nature of human behaviour, as described by Schill et al. (2019), but also the challenge of understanding environmental stewardship (Amel et al., 2017), which is often defined as implying a sense of responsibility for the state of the environmental system that we are part of (Chapin et al., 2009). Future studies could, therefore, benefit from including 'inner world' social factors that describe why people want to protect environment, such as values, identities or cultural beliefs (Chan et al., 2016; Ives et al., 2019), and how such social factors interact with environmental dynamics (Yletyinen, Tylianakis, et al., 2020).

The survey clearly indicates that conifer invasion management programs have not sufficiently reduced the barriers of control, since the costs and perceived inevitability of reinvasion stop even motivated landowners from controlling the invasion. Furthermore, given that many landowners acknowledged the cross-boundary nature of the invasion problem and adapted their control behaviour to the activities of other landowners, establishment of shared rules or collective action is required to achieve efficient landscape-level IAS control over the long term (see also Graham, 2019; Graham et al., 2019; Hulme, 2020). Our results suggest a favourable social setting for coordinating collective control action: there is a high level of agreement on the harmful effects of conifers among the landowners, and over one third of the landowners already discuss conifer invasion with each other (Graham, 2019; Niemiec et al., 2016, 2019; Ostrom & Ostrom, 2014).

Our modelling results show that when embedded in the dynamic social-ecological context, the aggregated impacts of some of the micro-level factors (in combination with the extent of invasion at the time control efforts begin) determine the control efficiency to the extent that higher level management strategies become largely irrelevant. This finding was evidenced by the fact that we detected no differences in control outcomes over the three management scenarios (Figure 5). Increasing the detail of social complexity in social-ecological models can lead to emergent, interactive mechanisms that increase the variety of environmental outcomes that the social-ecological system can produce (Yletyinen, Perry, et al., 2020). Therefore, the similarity of control outcomes over the three management scenarios result from the aggressiveness of the invasion and other factors (e.g. social network influence) being more influential in the system than those that were tested as management strategies (Supporting Information Figure S2 and Supporting Information Text ‘Supplementary experiments’). Social influence, landowners’ personal characteristics and views on invasive conifers’ financial impacts were correlated with landscape-level IAS control efficiency (Figure 4). In contrast, no significant correlation was detected between control efficiency and landowners’ probabilities of detecting conifers on their land as early as possible, or their ability to eradicate the IAS from their property (seedlings probability parameter; Figure 4). While these results were unexpected, they can, both in theory and by model design, be explained in that knowledge of a problem on its own rarely leads to pro-environmental behaviour (Amel et al., 2017; McLeod et al., 2015). Rather, drivers and barriers to landowners’ control behaviours emerge from a number of social factors (Amel et al., 2017; McLeod et al., 2015), as indicated by our survey results. These factors include the capacity to participate in the control efforts (e.g. perceived difficulty), motivation (e.g. attitudes, views on the impacts of IAS) and social and environmental features that prompt landowners to act (e.g. other landowners’ behaviours, invasion on own land; cf. McLeod et al., 2015). For example, early detection of invasion is useful only if the landowner decides, and is able, to control the invasive species in long term. In contrast to the study by Graham (2019), in our study, landowners’ action was voluntary and uncoordinated and no rules were established among landowners to address the invasion collectively as a public-good dilemma.

4.2 | Social-ecological interactions

Using the social-ecological simulation model allowed us to situate the micro-level social factors detected in the survey in a dynamic social-ecological context, in which management factors interact with each other and invasion dynamics. Our survey identified barriers to landowners’ participation in control efforts, which social-ecological processes may amplify, highlighting critical social-ecological feedbacks in the conifer invasion landscape. As the extent and density of conifer invasion increase in the landscape, control costs and labour increase such that fewer landowners can participate in control,
which leads to less successful control. This, in turn, perpetuates invasion which will, once again, increase the cost, producing a reinforcing feedback between invasion extent and the inability to control it. Given that ecological conditions alone can accelerate IAS spread (Aikio et al., 2010; Hulme, 2020), the increasing cost of control may cause a nonlinear shift in landowners’ ability to afford the cost of control. Furthermore, the survey showed that many landowners adjusted their control efforts to neighbours’ action. Some landowners decreased control efforts when neighbours increased theirs and vice versa. In the SEPIIM, these landowners ceased control on their property when most of their neighbours were participating in control efforts—a situation more likely in widespread invasions. This pattern in landowner participation can prevent spatial clusters of controlled areas from emerging. Further, the uncontrolled properties promote invasion, even if only a minority of landowners’ actions are conditioned on neighbours’ control behaviour. In addition, doing the opposite of neighbours contributes to slowing the spread of control behaviour through social network influence. These deleterious effects of neighbour influence and social network influence on widespread participation in control efforts are evident in the positive correlation between invaded area and social influence, and negative correlation between social influence and maximum control participation (Figure 4). Similar to prior research on favourable environmental and ecological factors for the spread of conifers, such reinforcing social-ecological patterns carry the risk of invasion-related social-ecological or ecological regime shifts (Shackleton et al., 2018). The most important implication of these modelling findings is that IAS management programs that focus solely on the ecological or social side of the invasion may allocate limited resources to managing ecological or social factors that are ineffective in the invasion context. Further, these findings emphasise the importance of managing the interactive processes (e.g. social network flows, feedbacks between control cost and invasion density) in the invasion landscapes, in addition to static ecological traits or social attributes. Similarly, management strategies that include both ecosystem health and socio-economic well-being are more likely to produce socio-ecological feedbacks that lead to efficient IAS control and that can be maintained over the time period needed (Larson et al., 2011). Future extensions to social-ecological models of invasion landscapes should, therefore, carefully integrate key social and ecological variables to detect reinforcing and balancing social-ecological processes that affect invasion landscapes over multiple spatial and temporal scales (Larson et al., 2011; Yletyinen et al., 2019). This is especially important due to the decadal time-scales required for successfully managing plant invasions (Hulme, 2020).

4.3 | Designing IAS management strategies

By examining the effects of micro-level social factors on IAS control efficiency, our results illustrate both the potential and the complexity of leveraging micro-level social drivers for improving control efficiency. Our findings emphasise that, similar to the necessity of ecological knowledge for environmental management (Hulme, 2020), successfully leveraging social context in IAS management requires detailed knowledge of the social dimension of the invasion landscapes, such as landowners’ adaptive behaviours and diversity in attitudes. In short, optimal IAS control programs require a carefully designed combination of management interventions that usually include ecological, social and economic aspects (Larson et al., 2011). The ‘right’ management combination depends, in turn, on how the individual tools of IAS management interact with each other, social context and the invasion dynamics. For example, providing advice and funding was the most effective lever in the management scenario that focused on halting the invasion at its sources in the ‘invasion sources’ experiment. Furthermore, while social interactions usually increase the diffusion of behaviours (Valente, 1996), in our study, the reason that social influence correlated negatively with efficient control action was due to the neighbour effect and almost two thirds of landowners not discussing conifer invasion with their peers (thus lacking social network connectivity). Finally, although we included three types of views on conifers’ effects, only landowners’ views on financial effects of the conifers correlated with the control efficiency. Of the three views, the landowners agreed most on the financial effects of conifers (Figure 3). Hence, how personal views affected control efficiency was affected both by what the view was (encouraging or discouraging to take action) and the diversity in this view among landowners (homogeneity of response). These examples and the potential presence of social-ecological feedbacks demonstrate that failure to consider either ecological or social processes in invasion landscapes can lead to suboptimal control programs and irreversible environmental change.

For invasive conifers in New Zealand, our experiments support a management scenario that is based on interventions targeting both social and ecological factors, namely: (a) starting control efforts in the early phase of the invasion, (b) establishing shared rules for participation (Ostrom, 2015) to avoid socially conditioned behaviour and to coordinate collective response due to the aggressiveness of the conifer invasion, (c) providing funding and advice, especially to landowners whose properties contain reproducibly mature trees and (d) targeting landowners’ views on the financial effects of the invasion. While each of these management interventions is likely to be effective on its own, our experiments suggest that their interactive effects can amplify the efficiency of conifer control on landscape level.

4.4 | Model limitations

Despite the use of detailed survey data and a robust ecological invasion model, our social-ecological model includes some simplifications that may affect the inferences we make from our simulations. IAS management is complex. Economic, environmental and societal changes occur over the time period modelled and might lead to changes in the social and ecological contexts in which the invasion occurs. For example, drastic increases in the extent of
invasion could trigger changes in landowners' and society's attitudes to invasive conifers (Thampi et al., 2018; van Wilgen & Richardson, 2014), and potentially provide social license for a shift to novel control techniques. The social-ecological model also excludes adaptive management of conifers, including cross-sectoral considerations that could improve long-term eradication success rates (Larson et al., 2011). For example, at the present stage of the conifer invasion, New Zealand could focus on early detection and within a few years change to a potentially more expensive scenario that focuses on prevention and seed sources in invasion. Finally, our study is based on a synthetic landscape, in which resilience of the landscape to invasion depends only on the invasion submodel and control behaviour. Nevertheless, our study provides an empirically informed example of how invasion landscapes function as social-ecological systems, showing how theoretical approaches to understand social-ecological interactions can contribute to designing on-ground management success.

4.5 Conclusions and outlook

The link between intended (e.g. gathered through social surveys) and actual behaviour has been externally validated in the literature (Chandon et al., 2005; Chang et al., 2009; Sun & Morwitz, 2010). By integrating social survey data with an ecological invasion model, and studying the emerging properties of social-ecological interactions at the landscape level, our study demonstrates how invasive species control occurs at a complex intersection of social and ecological processes. Our results show how micro-level social factors may contribute to the emergence of invasion landscapes. However, successfully leveraging social context in IAS management requires extensive knowledge of landowners' adaptive behaviours. Without knowledge of diversity of views and behaviours among landowners, and how management factors interact with each other and invasion dynamics, limited resources may be allocated to targeting social and ecological factors that do not influence invasion dynamics when in combination with the other factors of the control program.

Our results illustrate both the potential and complexity of leveraging micro-scale social drivers to improve the efficiency of invasive species control. To this end, a better understanding needs to be developed of how both landowner values, perceptions and collective behaviours translate into environmental change, and understanding social-ecological feedbacks of invasion landscapes. In the future, other sources of social and ecological complexity, such as the roles of industries and ecological interactions, will also need to be integrated into these models. A thorough understanding of how invasion landscapes emerge from constantly co-evolving social and ecological processes will significantly improve our ability to explain and manage IAS dynamics.

CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

AUTHORS’ CONTRIBUTIONS
J.Y. and P.S.-B. conceived the study idea; J.Y. designed the study, performed interpretation of results and wrote the manuscript; P.S.-B. designed and conducted the landowner survey; J.Y. and G.L.W.P. built the agent-based SEPIM; O.B. and N.M. built the invasion submodel. All the authors contributed to manuscript revisions and approved the manuscript for submission. The authors thank Duane Peltzer and the reviewers of this article for providing useful comments on the earlier version of this manuscript.

DATA AVAILABILITY STATEMENT
We used NetLogo 6.1.0. (Wilensky, 1999) for model programming and simulations, and R Studio version 1.1.463 coding environment for supporting SEPIM coding and analysis (R Core Team, 2018). NetLogo code for SEPIM and sample data for the landowner input file for SEPIM are available here: https://doi.org/10.17608/k6.auckld.14456286.v1 (Perry, 2021). The full survey dataset can be requested from the authors with consideration to survey respondents’ anonymity. Simulated, simplified landscapes and subsamples of landowners make the survey respondents unidentifiable in the model.

ORCID
Johanna Yletyinen https://orcid.org/0000-0002-7410-6794
George L. W. Perry https://orcid.org/0000-0001-9672-9135
Olivia R. Burge https://orcid.org/0000-0001-7719-6695
Philip Stahlmann-Brown https://orcid.org/0000-0003-4310-1103

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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