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RESEARCH ARTICLE

Modelling alternative management strategies of invasive tree species at the expansion front: *Ligustrum lucidum* as a case study

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Abstract

1. Managing invasive non-native species is a global challenge, especially for long-lived trees like *Ligustrum lucidum*, known for its detrimental effects on invaded ecosystems.
2. Using individual-based models (IBMs), we simulated different control methods on the population dynamics and range expansion propensity of the established population. Across different sets of simulations, we varied the number of life stages and sites targeted. We additionally investigated how changing the management strategy over time affected outcomes.
3. Controlling all life stages was essential to contain the expansion of *L. lucidum*. Removing both reproductive and non-reproductive stages was more than twice as effective as removing either saplings or reproductive stages only, especially if a high number of sites were targeted every year. The method of selecting sites for removal within the population was important if only saplings were removed; in which case targeting the most recently colonized sites was the most effective strategy. Finally, a strategy that switches after 5 years from controlling all stages to focusing exclusively on early life stages could be effective at reducing both the total population size and the area occupied.
4. *Practical implication*: This approach could be valuable when the availability of long-term resources for control is limited. The ability of IBMs to simulate various scenarios and assess outcomes at population and landscape levels enhances their utility for predicting invasive non-native species management success. It can be a solution to reducing the time and cost of fieldwork, helping to identify potential limitations of control actions.

KEYWORDS
biological invasions, conservation, control strategies, individual-based model, invasion containment, RangeShifter

1 | INTRODUCTION

Invasive non-native species (hereafter, INNS) pose a significant conservation concern due to their potential for having detrimental impacts on local biodiversity, causing major declines in native species and changes to the functioning of newly colonized ecosystems (Pyšek et al., 2020). The damages caused by invasive populations can induce economic losses in goods, services and production, leading to substantial mitigation costs (Diagne et al., 2021). Many well-established INNS cannot be completely eradicated, and need to be managed over the long-term to prevent further population expansion (Lambin et al., 2020). This containment usually necessitates treatment over large areas for a long time, which is generally constrained by the low availability of financial and management resources (Powell et al., 2023; Pyšek et al., 2020).

Moreover, an incomplete understanding of INNS population dynamics and their response to removal actions further complicates effective management (Funk et al., 2020; Woodford et al., 2016). In practice, many control or eradication efforts lack proper documentation, long-term planning and/or adequate monitoring for evaluating success. Even when adequate monitoring is in place, the results of management are likely to be evident only after many years of control. Such delays in ecological responses often result in unnecessary efforts and potential harm to ecosystems (Powell et al., 2023), especially when managing long-lived tree species that have the capacity to transform ecosystems significantly (Lamarque et al., 2011; Richardson et al., 2014).

To address the challenges of INNS management, such as uncertain population dynamics and long-term assessment, researchers combine empirical data, expert knowledge and theoretical assumptions to develop quantitative models that simulate population dynamics under different strategies of management. These models enable testing hypotheses in virtual environments, evaluating strategies and exploring scenarios that might be too costly or time-consuming to test in the field (Grimm & Railsback, 2005). Among these, individual-based models (IBMs) present a promising solution because they are flexible tools that can integrate demographic processes of species at various spatial and temporal scales (DeAngelis & Mooij, 2005; Grimm & Railsback, 2005). This not only aids in capturing the complexity of population growth but also facilitates the identification of knowledge gaps that may influence management recommendations. IBMs can be particularly useful for simulating the dynamics of long-lived tree populations, where density dependence often plays a more significant role than fecundity in shaping development and/or survival, driven by competition for resources. For example, the competition for light results in a disproportionate influence of large plants on the vital rates of smaller individuals (Craine & Dybzinski, 2013). This dynamic is especially relevant for invasive tree species, which may have a competitive advantage over native species, altering ecosystem structure. IBMs can indirectly consider this effect by incorporating different demographic parameters across different stages. Moreover, estimating demographic traits for tree species is challenging due to long generation times, and modeling plant dispersal is complicated by complex environmental and disperser behaviour effects (Rogers et al., 2019).

Individual-based models have been used in the past for predicting outcomes of alternative INNS management (Dominguez Almela et al., 2020; Lustig et al., 2019; Messager & Olden, 2018), but they have seldom been used for invasive plant management. Therefore, IBMs provide a great opportunity to quantify and inform the effectiveness of different control or containment strategies of INNS. In this context, we focused on the glossy privet *Ligustrum lucidum* (W. T. Aiton, Oleaceae), a problematic invasive tree species that is native to China (Montti et al., 2021). This tree was first introduced to Argentina in the 1900s, where it was widely planted for hedging, shade, shelter and as an ornamental plant in gardens. It is generally perceived as a cultural asset for ecotourism and outdoor recreational activities (Fernandez et al., 2020). However, when established, it forms mono-specific stands that dominate the entire local tree community. This results in a decline in biodiversity and changes in ecosystem functions (Fernandez et al., 2020). Containing (i.e. restricting or controlling) the spread of *L. lucidum* is one of the current objectives outlined in the National Strategy on Invasive Exotic Species by the Argentine Government (Ministerio de Ambiente y Desarrollo Sustentable, 2021) and different stakeholders like conservationist and researchers owing to its negative impacts on native biodiversity (Fernandez et al., 2020), there persists a requirement to formulate management strategies. Usually, control strategies for this species involve reducing its population through mechanical and/or chemical control and restoring by planting native species. The most effective overall strategy for controlling *Ligustrum lucidum* involves a combination of approaches: uprooting young saplings, while for mature trees, a combination of cutting techniques and immediate herbicide application is preferred (Lambin et al., 2020; Powell et al., 2023). Additional methods, such as grazing with cattle, are also employed (de Santiago et al., 2019). However, it's crucial to highlight that these approaches are still in their early stages and primarily confined to small-scale trials for limited periods. They have yet to be thoroughly evaluated in a broader landscape context, and their outcomes are currently in a developmental phase.

Here, using a tailored IBM and *Ligustrum lucidum* as example, we simulated the effects of alternative control methods on the population dynamics of an established invasive tree population of glossy privet. We varied the proportion of individuals and life stages targeted, and the location within the population where individuals were removed to identify optimal strategies for containing further range expansion. The simulations thereby address typical questions that practitioners face when designing management strategies to contain invasion (*where to control?*, *which individual stages to control?*, *whether* and *when to reduce or end control?*, Matzek et al., 2013), and will provide practical recommendations to fit management objectives that aim at containing the advance of invasive tree species and mitigate negative impacts on the native biodiversity.

2 | MATERIALS AND METHODS

We used a customized version of the individual-based spatially explicit modelling platform RangeShifter v2.0 (Bocedi et al., 2021; see also https://rangeshifter.github.io/). RangeShifter combines various demographic and dispersal models to simulate on an annual basis the spread of a species across a discretized landscape, and may be run either from a graphical user interface or in batch mode taking its inputs from text files. The input parameters required depend on the model choices made, and outputs may optionally be obtained at various summary scales: the whole range, local sub-populations and individuals. This customized version (RS_CONTAIN; https://github.com/RangeShifter/RS_CONTAIN) incorporates a new module for simulating the annual removal of INNS by some alternative strategies of management and optionally the damage caused by the INNS across the landscape.

2.1 | The model

2.1.1 | Population structure and fecundity

The population model assumed discrete classes of individuals constituting stage-structured overlapping generations. Based on our species knowledge, five population stages (S_0 to S_4) were defined by age and diameter by height (d.b.h) (Figure 1). Stage-specific demographic rates were computed from long-term data for *L. lucidum* collected from field surveys on our permanent plots in a subtropical montane forest in Argentina (see Supporting information: Text A1 for details). Seeds and seedlings (S_0) are not included in the population size at the start of each annual cycle (see Tables A1 and A2).

The probabilities of developing from S_n to S_{n+1}, (γ), were defined based on our knowledge of the species, given the absence of published empirical data (Table A1). Each individual could progress from one stage to the next, survive in the same stage, or die (Figure 1; Table A1). Stage-weighted density dependence was applied to survival only, whereby survival of younger stages was reduced in the presence of older stages, but not vice versa (Blundell & Peart, 2004; Green et al., 2014) (Table A3). The remaining parameter values applied were derived from published data and unpublished empirical field studies as described below. Seed production for each reproductive stage during the fruiting season peak was obtained using published and unpublished empirical data (Text A1; Figure A1).

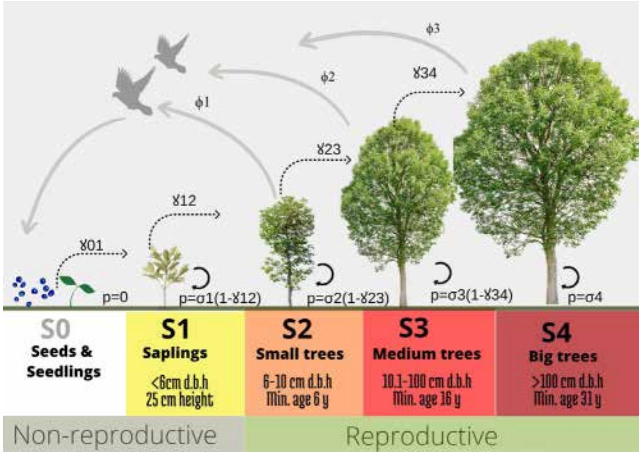

FIGURE 1 Flow chart of the stage-structured population of a *Ligustrum lucidum*, defined by age and diameter by height (d.b.h). (p) is the probability of remaining in stage n (Sn); (γ) is the probability of developing from Sn to $Sn+1$; (σ) is the survival probability and; (ϕ) is the fecundity of Sn.

2.1.2 | Survival rate of established stages

Based on demographic studies of neotropical tree species having similar size and potential shade tolerance (Green et al., 2014; Welden et al., 1991), we set the annual survival rate of saplings S_1 at low density to $\sigma_1 = 0.8$. Survival rates at low density for the three reproductive stages (S_2 to S_4) were substantially higher ($\sigma = 0.996$ to 0.999; Powell et al., 2024). Age at first reproduction (6 years corresponding to S_2), was derived from long-term census data of *L. lucidum* (see Supporting information: Text A1).

2.1.3 | Dispersal

Seed dispersal was modelled with a 2Dt kernel as a mixture of short- (k_1) and long-distance (k_2) kernels, where the probability density of seeds at a given distance depends on scale (u) and shape parameters (q) of each kernel (Clark et al., 1999). This mathematical function (2Dt kernel) is particularly suited for animal-mediated seed dispersal, as it captures both local and long-distance dispersal events driven by variable animal movement patterns. The long-distance dispersal process simulates active density-independent emigration involving in our example case fruit-eating birds, which is the most common way of dispersion (Fernandez et al., 2020). Regurgitation of seeds by birds leads to short-distance dispersal (k_1, $u_1 = 11.34$, $q_2 = 5.58$) at high probability (0.85), and defecation of seeds at longer distances (k_2, $u_2 = 7.52$, $q_2 = 0.25$) with lower probability (0.15; Powell & Aráoz, 2018).

2.2 | Spread dynamics

To examine the invasion process and investigate how different parameter assumptions can affect range expansion, we followed the approach of Plenderleith et al. (2022), modelling a tree population at a small spatial scale in a homogeneous theoretical landscape. We assume that from the start of the simulation, the species is free to grow and spread after an establishment phase. We implemented simulations on a 20 ha artificial landscape comprising a grid of 500 cells of 20 m resolution, which is one typical size plot in which do field-work in a dense forest, with an extent of $x = 2000$ m, $y = 100$ m, all of which was suitable habitat for the *L. lucidum*. At the start of the simulation, 20 individuals were placed into two cells of the bottom row and the first two columns of the grid representing 0.4% of the total area, with the other cells empty.

Equilibrium densities within local sub-populations emerge from the dynamics produced by model parameters including 1/*b*, which determines the shape of the relationship between fecundity and local population density. Here, 1/*b* = 300 individuals/ha (Montti et al., 2016), which, together with the other parameters (fecundity, development, survival, dispersal), yielded a local maximum population size of 300–350 reproductive trees at equilibrium, consistent with field estimates (Montti et al., 2016). The occupied cells were initialized with 10% of individuals in S_1, 60% in S_2, 20% in S_3 and 10% in S_4 to replicate a naturally occurring *L. lucidum* population in a forest with a high proportion of younger trees. This implies a forest where most trees are between 1 and 20 years old, often found in areas with recent disturbance or natural regeneration, which is common for *L. lucidum* invasion (Montti et al., 2016). We simulated six replicates of range expansion for 350 years to allow the equilibrium range expansion dynamics to be reached. This duration accounts for the long lifespan of *L. lucidum*, which can exceed 100 years (Fernandez et al., 2020), and allows for at least two complete generational cycles to capture stable patterns in population dynamics and dispersal. Model outputs were generated every 10 years to follow the number of individuals across stages S_1 to S_4 in each cell of the grid. The mean rate of range expansion was calculated across replicates from the number of years taken for the established population (S_1 to S_4) to reach the limit of the landscape.

2.3 | Management strategies design

To evaluate potential methods for containing *L. lucidum* expansion into new areas or limiting its population growth in existing areas, the spread dynamics model was run twice for 100 years to provide two replicate baseline stage-structured spatial distributions of *Ligustrum* populations at and behind the invasion front. The population covered just over half of the landscape, thereby providing scope for the population to continue to expand or to be contained by simulated management. We evaluated the effect of control strategies before seed dispersal in a series of three experiments with different combinations of life stages and the number and location of sites targeted (Table 1). We assumed that all sites (hereafter referred to as cells) in the landscape were accessible for control. Each experiment was run for 30 years, and each combination of experimental factors was replicated twice. A '*no-control*' strategy was also simulated, in which no clearance of *Ligustrum* was applied at any time.

Individuals in selected cells were subjected to a stage-dependent probability of removal, based on the assumption that in the field, almost no large reproductive trees and only a low number of small reproductive trees would be missed and thus not felled by managers. Accordingly, the removal probabilities for reproductive stages S_2, S_3 and S_4 were held constant in all experiments at 0.95, 0.97 and 0.99, respectively, while those of saplings (S_1) were 0.80 or 0.90 depending on the experiment. The number of cells targeted for removal in any year was 25, 50, 75 and 100, which respectively represented 8.5, 16.9, 25.4 and 33.8% of the initial occupied cells (mean = 295.5 cells). As different locations within the established population can be targeted in the field and based on actual stakeholder questions and current fieldwork capacities, we tested three methods for selecting cells: (1) random over the whole landscape, (2) biased towards those most recently colonized cells and (3) stratified by local population size in the cell.

In *Experiment 1*, we evaluated the effect of removing different life stages and varying the number of cells targeted each year for 30 years. Either non-reproductive saplings only (S_1), reproductive trees only (S_2 to S_4) or all (S_1 to S_4) were removed at two spatial levels (low or high number of targeted cells, see Table 1). We assumed that the effort required to remove all saplings in one cell was the same as the effort required to remove reproductive trees, and half the effort required to remove all four stages; hence, the number of cells targeted for control was halved when all four stages were removed. Additionally, two levels of threshold density were applied when only saplings were removed (125 and 250 ind/ha), which represented the minimum density in a cell to qualify for potential selection; otherwise, only one level (25 ind/ha) was applied to control all stages.

In *Experiment 2*, as combining control efforts for all stages is often more cost-effective in the long run than addressing each stage separately, we remove all stages (S_1 to S_4) to evaluate the effect of varying the number of cells targeted per year (Table 1). The aim was to estimate the lowest number of cells to be removed that would be sufficient to contain the spread of *L. lucidum* invasion.

In *Experiment 3*, we examined whether switching from removing all stages to removing only S_1 and S_2 after 5 years of removal would maintain effective control of the population over 15 years while decreasing the field-work effort. Individual-level data after 5 years of control were retained and converted to initialisation files for these new simulations. Two replicates of each of the simulations described previously (total 96) were run for 10 years starting from the 48 initialised populations. All other management factors remained unaltered. The data from years 5 to 15 of equivalent simulations from Experiment 2 acted as the 'control' regime, that is, continuing to remove all four stages for a further 10 years.

2.4 | Sensitivity analysis

The sensitivity analyses were performed for Experiments 1 and 2, excluding Experiment 3. In short, demographic and dispersal parameters were modified by ±0.1. The sensitivity analysis confirmed that the main results were robust to small variations in the different model parameters (Supporting Information: Text A2 and Tables A7.1 and A7.2 and Figures A7.1 to A7.20).

TABLE 1 Factorial design of simulated management experiments.

Factor	Number of levels	Level meaning
Experiment 1		
Initial population	2	20,817 individuals across 302 cells and 20,321 individuals across 289 cells
Stages controlled	3	1 = saplings only; 2 = reproductive trees only; 3 = saplings and reproductive trees
Cell sampling (method)	3	0 = random; 1 = recently colonized cells; 2 = cells with the largest populations
Number of target cells	2	Two levels 'low' and 'high', depending on 'Stages controlled': for (1) saplings only or (2) reproductive trees only, 50 or 100 cells for (3) saplings and reproductive trees, 25 or 50 cells
Threshold density	2	Two levels when saplings only were controlled: 125 or 250 ind/ha
Removal probability for saplings	2	1 = 80%; 2 = 90%; applied only if 'Stages controlled' is 1 or 3
Count error (coefficient of variation)	1	One level depending on the stage controlled: for saplings only 20%; for reproductive trees only, 5%; for saplings and reproductive trees, 10%
Reps	2	
Total simulations	**172**	
Experiment 2		
Initial population	2	20,817 individuals across 302 cells and 20,321 individuals across 289 cells
Stages controlled	1	All (reproductive and saplings)
Cell sampling (method)	3	0 = random; 1 = recently colonized cells; 2 = cells with largest populations
Number of target cells	4	25, 50, 75 or 100
Removal probability for saplings	2	1 = 80%; 2 = 90%
Count error (coefficient of variation).	1	10%
Reps	2	
Total simulations	**96**	
Experiment 3		
Initial population	2	20,817 individuals across 302 cells and 20,321 individuals across 289 cells
Control strategy	1	All stages for 5 years, then S_1 and S_2 only for a further 10 years
Reps of first 5 years	2	
Cell sampling (method)	3	0 = random; 1 = recently colonized cells; 2 = cells with largest populations
Number of target cells	2	50, 100
Control probability for saplings	2	1 = 80%; 2 = 90%
Reps	2	
Total simulations	**96**	

2.5 | Analysis of the outputs

Output data were summarized in terms of the number of occupied cells, that is, cells holding established trees (S_1–S_4), and the number of individuals in each stage over time or at the end of 30 years of management. Seeds and seedlings (S_0) were not considered. The most important factors in each experiment were identified by fitting the summary statistics to ANOVA models, and comparing the variance explained by each experimental factor and their first-order interactions (SAS v9.3).

3 | RESULTS

3.1 | Initial expansion dynamics of *Ligustrum*

The modelled invasive tree population increased quickly over time, producing a large number of saplings, until it reached the limit of the landscape after 167 ± 5 years. Thereafter, the population size briefly declined, but increased again at a slower rate to stabilize at year 350 (Figure 2b). The population was mainly composed of saplings (S1) and the other stages each represented less than 20% of the population (Figure 2c).

3.2 | Experiment 1: Targeting different life stages

The choice of stages targeted for removal was the most important factor affecting cell occupancy after 30 years relative to no control (Table 2, Table A4). Removing both reproductive and non-reproductive stages was more than twice as effective as removing either saplings or reproductive stages only, especially if a high number of cells was targeted every year (Figure 3a). The selection method was important if only saplings were removed; in which case selecting the most recently colonized cells was the most effective option (Figure 3b).

3.3 | Experiment 2: Number of cells targeted and removal probability of saplings

When removing all stages, the number of cells targeted accounted for 80% of the variance in the change in cell occupancy after 30 years relative to no-control, followed by the removal probability of saplings (10%), and their interaction (3.5%; Table 2, Table A5). At higher numbers of cells selected, the additional effect of the removal probability of saplings became greater, such that the number of occupied cells was reduced by 61.2% (~180 cells) relative to no-control at the highest levels of cells targeted and removal probability of saplings (Figure 4a). The method by which cells were selected appeared to have only a limited effect on the outcome on cell occupancy (Table 2). Despite the effect of this strategy remaining fairly consistent from 10 to 30 years of control (i.e. occupancy by reproductive trees was 68% to 77% lower than with the 'no-control' strategy), the first 5 years appeared to be the key period in reducing the spread (Figure 4b). After this time, control was useful only if all population stages were considered (Figure 5, Table 2) emphasizing the necessity of multiple interventions over time. Despite reductions in the number of older established reproductive trees (S_3 and S_4), saplings (S_1) and young reproductive trees (S_2) were still present, resulting in no overall difference in occupancy compared with the no-control strategy, where the occupied cells were dominated by S_3 and S_4 trees (Figure 5).

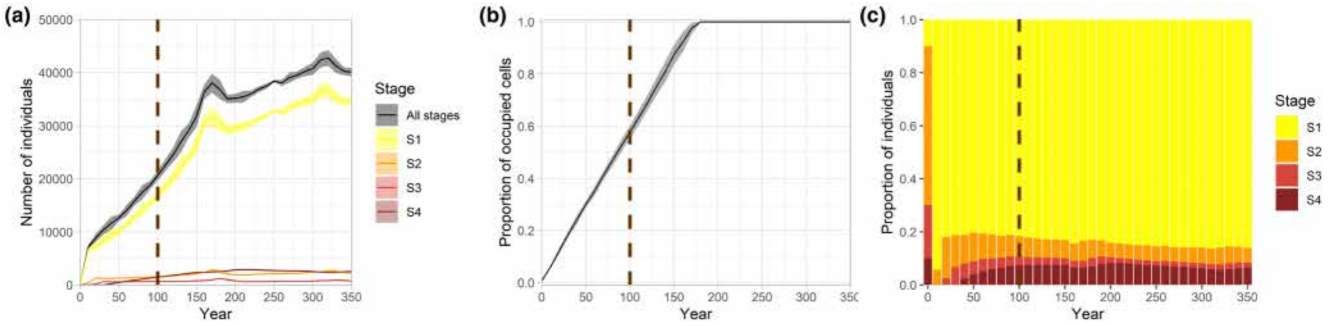

FIGURE 2 Temporal dynamics and composition of a *Ligustrum lucidum* population during range expansion (number of replicates = 6) S1 = saplings, S2 = small trees, S3 = medium trees and S4 = big trees. (a) Mean number ± SE of individuals (S1–S4) over time; (b) Mean proportion ± SE of occupied cells in the landscape over time; (c) Mean proportion of the different stages over time. The vertical dashed line represents the initial population composition used to run the experiments.

TABLE 2 Principal sources of variance explained (%) in the change in cell occupancy after 30 years relative to no-control in Experiments 1 and 2, and in cell occupancy after 15 years in Experiment 3.

	Management-related factors				
	Selection method	No. of cells	Stages	Control probability for saplings	Switching culled stages
Experiment 1	6.8	10.0	**66.3**	3.5	n/a
Experiment 2	2.5	**80.2**	n/a	10.4	n/a
Experiment 3	3.2	**69.7**	n/a	14.5	7.5

Note: Bold highlighted the factors that accounted for the most variance.

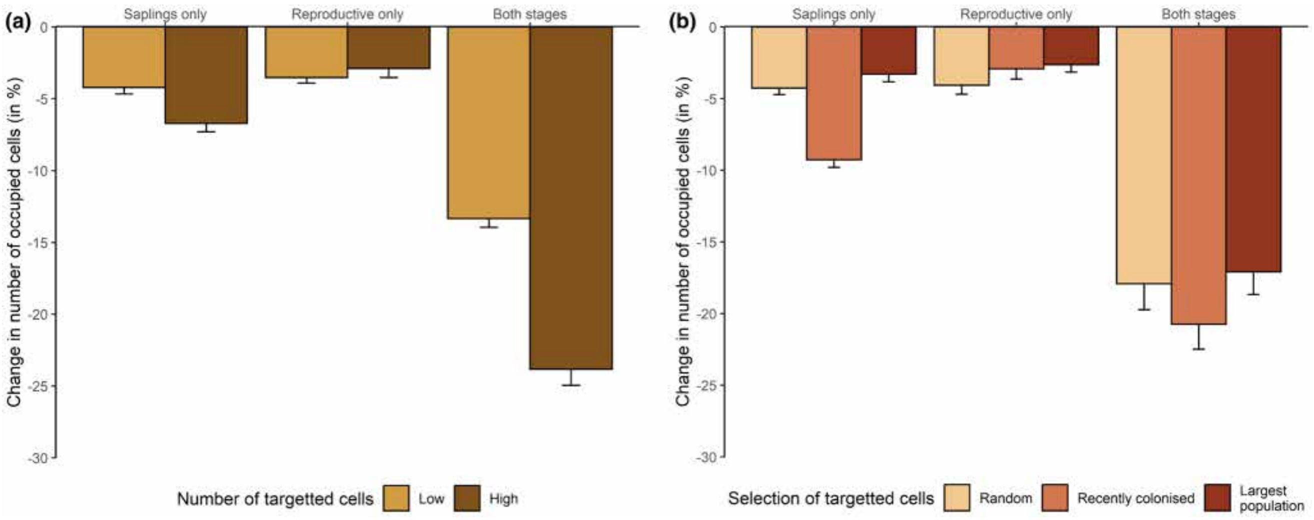

FIGURE 3 Percentage of change in cell occupancy relative to no-control for the invasive *Ligustrum lucidum* after 30 years in relation to (a) the stages removed and the number of cells targeted per year ('low':50 or 'high': 100 cells if saplings alone or reproductive trees alone are targeted, whereas 'low' is 25 cells and 'high' is 50 cells if both saplings and reproductive trees are targeted) and (b) the stages removed and the cell selection method applied. Predicted means are averaged across all other factors; error bars show ±1 SE.

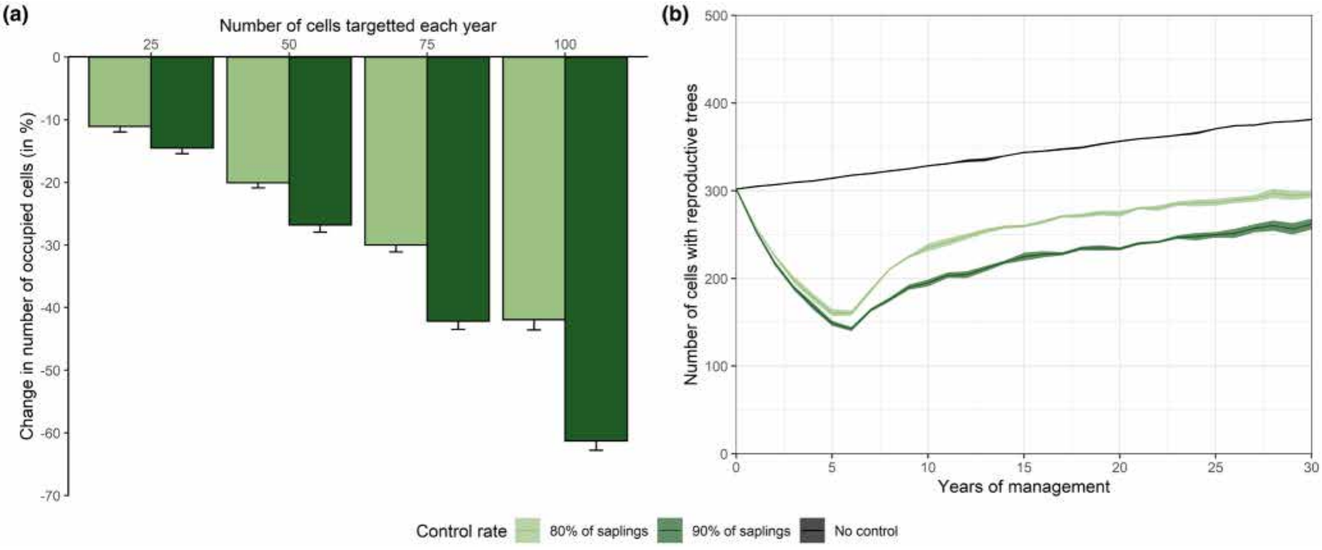

FIGURE 4 (a) Change in cell occupancy by reproductive trees relative to no-control for *Ligustrum lucidum* in relation to the number of cells selected for culling and the cull rate of saplings achieved. Predicted means are averaged across all other factors; error bars show ±1 SE. (b) Temporal change in *L. lucidum* occupancy by reproductive trees over 30 years of management at two levels of sapling removal rate. Green lines show occupancy when 75 cells are selected for control each year, and data are averaged over a method of cell selection. The black line represents the change in occupancy when control was not applied.

3.4 | Experiment 3: Effect of switching the control regime after 5 years

There was no difference in the number of occupied cells and total population size at year 5, but after 15 years, the control strategy accounted for 61% of the variance in the total population size and only 7.5% of the variance in cell occupancy (Table 2; Table A6).

Removal of S$_1$ and S$_2$ only after 5 years resulted in an increase in the number of cells occupied by reproductive trees in year 15 (Figure 6a), which was consistent across the number of cells selected and the removal probability for saplings. In contrast, when the number of cells selected was relatively low, switching to removing only S$_1$ and S$_2$ led to a substantial reduction in the total population size (Figure 6b). There was no remarkable difference between strategies when the number of cells selected was high (Figure 6b).

In the switching strategy (removing only S$_1$ + S$_2$), the number of cells in which S$_3$ and S$_4$ were present remained stable rather than declining, but the increase in the number of cells where S$_2$ trees were the oldest stage present was reduced relative to continuing to control all four stages (Figure 7). Switching also led to slightly

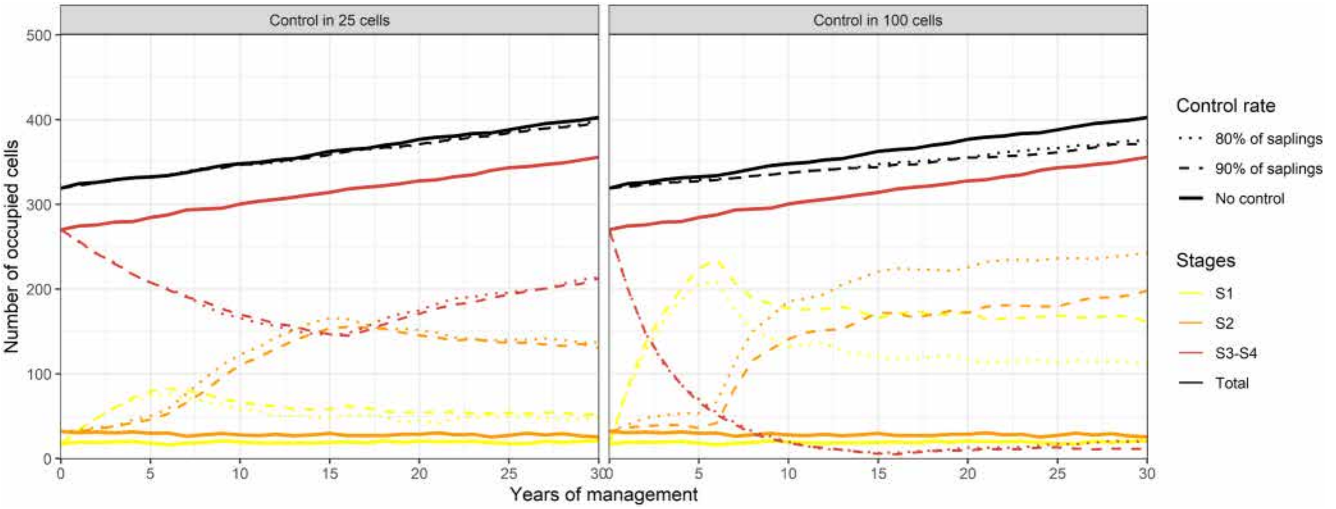

FIGURE 5 Changes in cell occupancy classified by the oldest stage(s) present in the cell during 30 years of management (Experiment 2) at two levels of sapling removal rate (0.8 or 0.9) and in relation to the number of cells selected for control (25 or 100). Solid lines represent cell occupancy under no-control. The dashed and dotted lines represent the cell occupancy when control is applied.

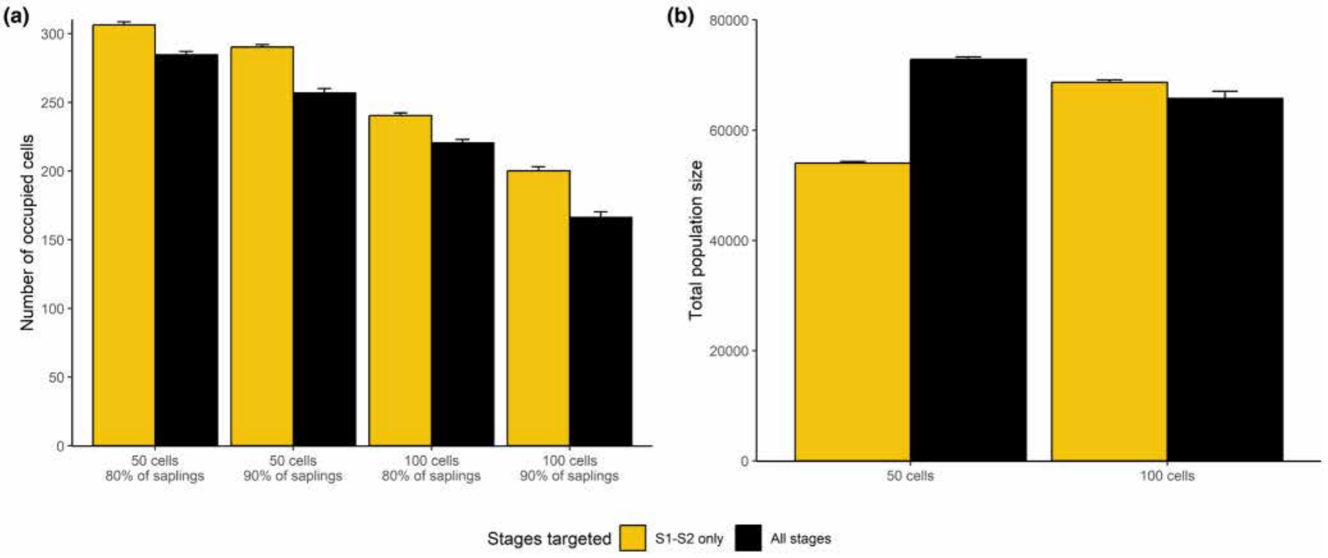

FIGURE 6 Effect after 15 years of removing only stages 1 and 2 from years 5 to 15 versus continuing to remove all four stages on (a) the number of occupied cells by number of cells controlled (50 or 100) and sapling control rate (80% or 90%) and (b) the total number of individuals (saplings and reproductive trees) by number of cells controlled (50 or 100). Data show marginal means averaged across all other factors, initialisation replicates and simulation replicates; error bars show ±1 SE.

larger decreases in the number of cells occupied by saplings only (Figure 7).

4 | DISCUSSION

Population modelling has been increasingly applied to biological invasions, especially to support management decisions (Buchadas et al., 2017). Here, we modelled for the first time the invasion dynamics and the potential management of a tree species population with age-dependent demography and dispersal parameters from empirical data, thus providing a series of novel insights to inform researchers and managers during the decision-making process. In particular, we showed how the local expansion of one of the most widely distributed invasive trees globally can be contained using specific control strategies, thereby providing useful directions to stakeholders about the spatial extent and the stages that should be targeted (García-Díaz et al., 2021; Powell et al., 2023).

Containing invasive species abundance is difficult to achieve in practice. Our simulations showed that removing all reproductive trees (S2 to S4), as well as saplings (S1), was the most effective strategy to contain the spread and abundance of invasive trees at a local scale, rather than focusing on saplings alone which are often easier and/or cheaper to target (Pichancourt et al., 2012).

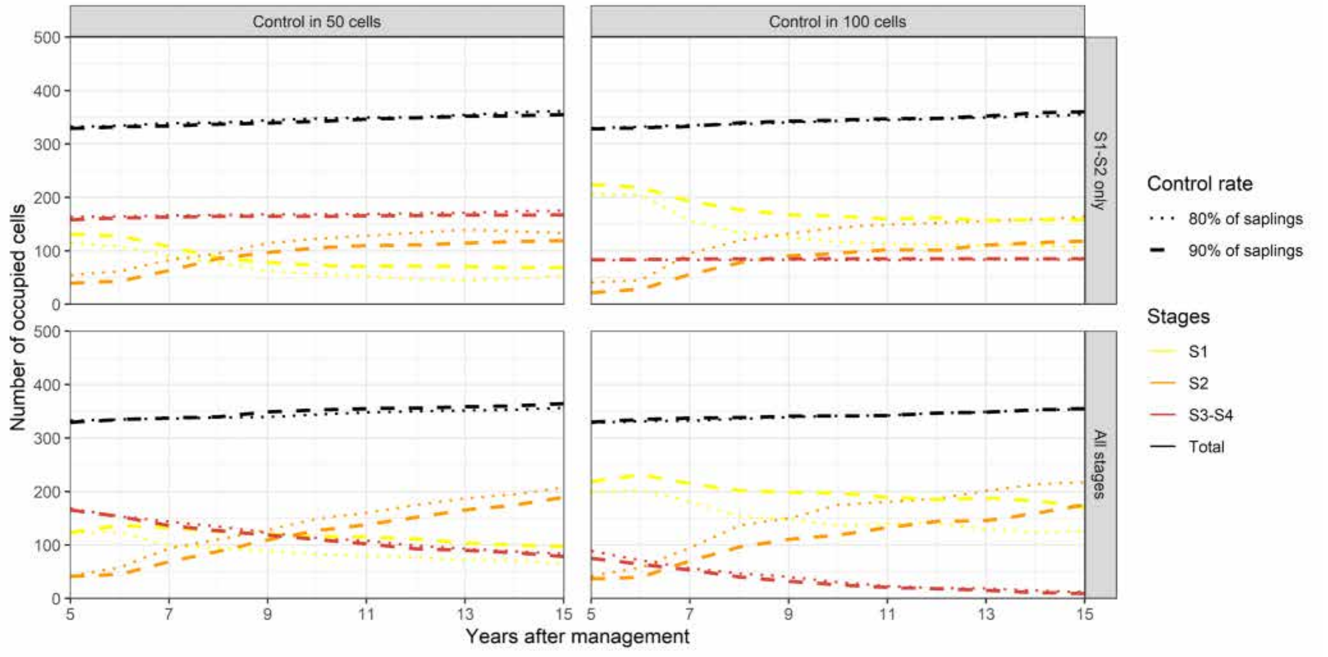

FIGURE 7 Comparison by number of cells controlled (50 or 100) and sapling control rate (80% or 90%) of the change in stage-specific cell occupancy from years 5 to 15 between (below) continuing removing all four stages, and (above) removing only stages 1 and 2 from year 5 onwards. Data show averages across replicates for simulations in which the method of patch selection was weighted towards the largest population sizes.

Our results complement two previous studies that showed that targeting older and more fecund plants farther from the expansion front might be more effective than targeting younger plants closer to the front to contain invasion (Travis et al., 2011) because seed production could be more efficiently reduced (Ramula et al., 2008). Accordingly, accounting for fruiting seasonality (i.e. implementing control strategies before fruits appear) could be beneficial, by ensuring that a new cohort of seedlings would not benefit from the new environmental conditions created by the clearance of larger trees (Maan et al., 2020). Despite those promising results, we highlight that *L. lucidum* is characterized by high production of seeds and seedlings and effective dispersal, resulting in a large proportion of saplings during the early years of invasion (up to 80% of the population size in our model), and a high number of mature reproductive trees during later stages of the invasion. This matches qualitatively our observations of population structure in field conditions where the dominance of the species ultimately changes forest microclimate, depressing the regeneration of native species (Fernandez et al., 2020) and creating a community that is close to a monoculture.

The rate at which saplings are removed (i.e. the cull rate in selected cells) played a crucial role in containment outcomes for the number of sites controlled (see Figure 4). Therefore, we recommend using time and resources to train technicians to recognize the different development stages of the targeted species to remove and to not miss them (especially saplings) which improves the performance of removal rate of failure, mainly in biodiverse forest densely populated with saplings of many species. Our results suggest that such training to catch all individuals in the field can help to increase the performance of the clearance operation. A second visit by experienced practitioners to remove any missed individuals could be another potential option after the initial removal has been completed. Further research is required to generate specific recommendations, which will inevitably depend on resources availability, the abundance of the INNS -in our case, *Ligustrum lucidum*- , and management objectives (Buckley & Han, 2014; Hulme, 2006).

Contrastingly, the methods by which cells were selected had only a limited effect on the outcomes of the control strategies (Figure 3b). This may be in part because of the large number of occupied cells at the start of simulations. Moreover, it was assumed that all cells (sites) are accessible, which is often not the case in the field. Additionally, we assumed a homogeneous landscape, which may not fully capture the spatial variability found in real ecosystems, such as differences in habitat suitability or accessibility. Thus, in real situations, we suggest increasing the number of sites controlled in accessible areas while also accounting for landscape heterogeneity, which can affect the effectiveness of control strategies.

Our results showed that targeting a high number of cells for *Ligustrum lucidum*, removal was effective in controlling older reproductive trees (Experiment 2). Simultaneously, our results suggested that younger individuals could potentially benefit from the reduction in intraspecific competition and become more abundant (Craine & Dybzinski, 2013). However, there are two important caveats. Firstly, whilst it can be assumed that the stage weights matrix applied in the model to determine the local level of density-dependent survival is qualitatively reasonable; its parameters were set based on expert knowledge, as field data are not yet published. Secondly, the model simulates only the *Ligustrum lucidum* itself; interactions with native species in the forest are not represented, and removal of this target INNS might increase the survival rates of seedlings and saplings of native species in cells from which older trees have been removed. Future research should focus on the dynamics of these interspecific interactions. Considering our findings, we suggest planting native species a year after control to boost the recovery of native trees and biotic interactions (Chazdon & Guariguata, 2016; Schuster et al., 2018). This low-risk strategy enhances conservation by promoting the recovery of native biodiversity through the removal of INNS and replanting local species, providing dual social and environmental benefits.

In the same way, a flexible control strategy (Experiment 3) suggests that control may be most efficient overall if some sort of mixed approach is applied. In our case, a flexible control strategy could lower overall INNS populations but not necessarily reduce cell occupancy. The medium- to long-term results will depend on when exactly the strategy shifts from removing all stages to removing only specific stages, which stages are targeted after the switch and whether switching allows more (or fewer) cells to be selected each year. In this study, a single control strategy was run as a separate simulation, initialising the second and any subsequent phases from individual-level data saved at the end of the previous phase. The next step would be to adapt the model (RS_CONTAIN software in our case) to incorporate a mixed control strategy, as well as incorporate the interaction between species, in a single simulation if the full potential of the software is to be realized.

Even though our IBMs were not totally calibrated with real data from published information, our findings broadly match the qualitative expectations according to demographic dynamic populations of trees (Begon et al., 2006), establishing the foundation on which to develop and redefine future models. While there is confidence in our predictions, we would welcome further empirical studies collecting demographic data. The uncertainty of model parameters and processes can sometimes result in inappropriate inferences or unreliable outputs (Sofaer et al., 2018; Wilson et al., 2005). Incorrect outputs may lead to wrong conclusions that latterly turn out to have unintended negative consequences for INNS management (García-Díaz et al., 2019). The effective uptake and application of our model outputs to select the best strategies for INNS management would require good communication between researchers, managers and modellers as well as consistent monitoring to assess if these actions result in the desired management outcomes (García-Díaz et al., 2021). Despite these issues, the robustness of our model, as tested with multiple sensitivity analyses, simulates the outcome of strategies to control populations of INNS, making it a powerful tool to provide clear guidelines for INNS-management.

In summary, despite the limitations and constraints of IBM (e.g. high requirement of computational power and time, need for detailed and accurate data, defining assumptions that generate uncertainty, outputs not easy to interpret or communicate to non-specialist audiences), we offered insights into controlling invasion processes and demonstrated that IBMs are potentially useful tools for management of INNS. For our targeted species we strongly suggest (1) controlling all stages at the same time (from saplings to adults), (2) targeting recently colonized areas by removing saplings with technicians who have experience in sapling identification and (3) developing collaborative research to increase the degree of detail and realistic outputs in models addressing decision-making and conservation problems. Our suggestions can be easily transferrable and testable with our approach across a variety of INNS.

AUTHOR CONTRIBUTIONS

Lia Montti, Aurore Ponchon, Stephen C. F. Palmer and Priscila A. Powell developed the initial ideas; Stephen C. F. Palmer, Aurore Ponchon and Lia Montti led experimental simulations and analysed the data. Lia Montti and Aurore Ponchon led the writing, with extensive inputs from Stephen C. F. Palmer, Priscila A. Powell, Justin M. J. Travis and David R. F. P. Burslem. All authors participated in the interpretations of data and critically revised the draft giving final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70012.

DATA AVAILABILITY STATEMENT

The data supporting this study are available via NERC EDS Environmental Information Data Centre: https://doi.org/10.5285/c3295206-052a-4c87-911a-75d357791b5c (Powell et al., 2024), via Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET): http://hdl.handle.net/11336/251732 (Montti et al., 2025).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: Biological invasions, Control strategies, Conservation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text A1. Biological traits of the target species used to calculate parameters.

Text A2. Sensitivity analysis.

Figure A1. Relationship between number of seeds and dbh for *L. lucidum*: Adjusted $R^2 = 0.418$, $F_{1,20} = 16.1$, $p < 0.001$.

Table A1. Annual transition matrix used in RS_CONTAIN.

Table A2. Parameter values used within the model.

Table A3. Stage weights applied to density dependence in survival.

Table A4. Partitioning of the variance (%) in the number of occupied cells relative to no management after 30 years between the experimentally manipulated factors and their first-order interactions in Experiment 1.

Table A5. Partitioning of the variance (%) in the number of occupied cells relative to do management after 30 years between the experimentally manipulated factors and their first-order interactions in Experiment 2.

Table A6. Partitioning of the variance (%) in the number of occupied cells after 15 years between the experimentally manipulated factors and their first-order interactions in Experiment 3.

Table A7.1. Perturbation of parameters for sensitivity analyses of Experiments 1 and 2.

Table A7.2. Variance explained (%) in the number of occupied cells relative to no management after 30 years by perturbation of a single parameter or group of parameters in sensitivity analyses of Experiments 1 and 2.

Figure A7.1. Influence of perturbing sapling survival by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.2. Influence of perturbing adult survival (by altering mortality by ±10%) on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.3. Influence of perturbing adult fecundity by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.5. Influence of perturbing *1/b* by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.6. Influence of perturbing the proportion of seeds dispersing using kernel 1 by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.7. Influence of perturbing parameter *u* for kernel 1 by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.8. Influence of perturbing parameter *p* for kernel 1 by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.9. Influence of perturbing parameter *u* for kernel 2 by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.10. Influence of perturbing parameter *p* for kernel 2 by ±10% on the effect of the stages controlled to determine the number of occupied cells relative to no management after 30 years (Experiment 1).

Figure A7.11. Influence of perturbing sapling survival by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.12. Influence of perturbing adult survival (by altering mortality by ±10%) on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.13. Influence of perturbing adult fecundity by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.14. Influence of perturbing survival stage weights by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.15. Influence of perturbing *1/b* by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.16. Influence of perturbing the proportion of seeds dispersing using kernel 1 by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.17. Influence of perturbing parameter *u* for kernel 1 by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.18. Influence of perturbing parameter *p* for kernel 1 by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.19. Influence of perturbing parameter *u* for kernel 2 by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

Figure A7.20. Influence of perturbing parameter *p* for kernel 2 by ±10% on the effect of the number of cells selected for removal and the control rate of saplings to determine the number of occupied cells relative to no management after 30 years (Experiment 2).

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