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RESEARCH ARTICLE

Remove saplings early: Cost-effective strategies to contain tree invasions and prevent their impacts

Jaime Moyano[1] | Pablo García-Díaz[2,3] | Barbara Langdon[4,5] | Stephen C. F. Palmer[2] | Paul Caplat[6] | Xavier Lambin[2] | Aníbal Pauchard[4,5] | Martin A. Nuñez[1,7]

[1]Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina; [2]School of Biological Sciences, University of Aberdeen, Aberdeen, UK; [3]Instituto de Ecología Regional (UNT-CONICET), Tucumán, Argentina; [4]Laboratorio de Invasiones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile; [5]Institute of Ecology and Biodiversity (IEB), Santiago, Chile; [6]School of Biological Sciences, Queen's University Belfast, Belfast, UK and [7]Department of Biology and Biochemistry, University of Houston, Houston, Texas, USA

Correspondence
Jaime Moyano
Email: mjaime@comahue-conicet.gob.ar

Xavier Lambin
Email: x.lambin@abdn.ac.uk

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Abstract

1. There is an urgent need to design management strategies to reduce invasive species spread and impact, but the large spatial and temporal scales of most biological invasions make them challenging environments in which to conduct field studies. In this context, simulation models can play a key role in informing invasive species management. Woody plants are among the most harmful invaders, yet an evidence base to support different management objectives for these species remains poorly developed. Pines (*Pinus*) have been intensively studied, in terms of demography, dispersal, spread and impact, which makes them an ideal study system to model invasions.
2. Using a multiyear database of observations of an invasive population, we employed an approximate Bayesian computation to fit an individual-based spatially explicit model to compare management strategies to reduce the spread, population size and impact of a woody invader, *Pinus contorta* (pine hereafter), on grasslands in Patagonia. We simulated a pine population spreading from a plantation into a grassland over 50 years. Annual control actions in the grasslands started as soon as pines started spreading (when the pines from the plantation become reproductive) or were delayed at 10-year intervals. For control actions, we targeted different pine life stages, prioritized different locations in the landscape and explored a wide range of available budgets.
3. Removing saplings was the most cost-effective way to reduce pine spread and population size, whereas reducing management delay had a stronger effect on minimizing pine invasion impact on native grassland productivity. Focusing only on invasive adults was ineffective because it was costly, and it allowed a build-up

in the population size of other stages which soon became adults (and started spreading seeds).

4. *Synthesis and applications*: Our highest-ranking strategies represent management actions to start implementing in the field as part of an adaptive management plan that iteratively evaluates the validity of our simulation model and updates the management recommendations. Our study can be applied to guide management of invasive pines and replicated with any invasive woody species with sufficient data.

KEYWORDS

decision criteria, exotic species, impact-based management, invasion management, *Pinus*, population control, process-based models

1 | INTRODUCTION

Biological invasions are a major component of global change, producing massive negative economic (Diagne et al., 2021; Moodley et al., 2022; Roy et al., 2023) and ecological impacts worldwide (Pyšek et al., 2020; Roy et al., 2023; Vilà et al., 2011). Given these impacts, the management of invasive non-native species (INNS, hereafter) has become a priority to mitigate their negative effects (Lenzner et al., 2024; Early et al., 2016; Turbelin et al., 2017). However, resources to tackle INNS are relatively limited, especially compared with other pressing global environmental priorities such as mitigating climate change, reducing pollution and reducing deforestation. This implies that those limited resources need to be invested wisely to achieve INNS management objectives. Yet, while substantial research has assessed the economic costs of biological invasions (Diagne et al., 2021; Moodley et al., 2022; Roy et al., 2023), few studies assessing control actions for INNS consider the cost of management (Kettenring & Adams, 2011). Therefore, it is essential to design management strategies for INNS that are effective in containing or reducing their range and ecological impacts while efficiently using the limited resources available (Epanchin-Niell, 2017; Epanchin-Niell & Hastings, 2010).

Invasive trees are becoming a major threat for the conservation of (previously) treeless ecosystems, such as grasslands, shrublands and wetlands (Le Maitre et al., 2011; Nuñez et al., 2017; Shackleton et al., 2014; Simberloff et al., 2010). Non-native tree species are being widely planted over large treeless areas across many countries for production purposes (Essl et al., 2010; Richardson et al., 2011; Shackleton et al., 2014), and, more recently, for carbon sequestration (Bond et al., 2019; Feng et al., 2016; Lewis et al., 2019), a change in land use that causes numerous negative impacts (Moyano, Dimarco, et al., 2024). In particular, the replacement of naturally treeless ecosystems by non-native tree plantations reduces native biodiversity (Prangel et al., 2023; Veldman et al., 2015), ecosystem services (Prangel et al., 2023) and local water yield (Alvarez-Garreton et al., 2019; Jackson et al., 2005), while increasing fire severity (Paritsis et al., 2018; Stevens & Bond, 2024). These negative impacts are compounded by the expansion of invasive tree distributions beyond plantations to native ecosystems (Le Maitre et al., 2011; Nuñez et al., 2017). Therefore, there is an urgent need to design management strategies for invasive tree populations.

One key aspect in the design of management strategies is to define the objective, which can range from eradication of an INNS to containment of spread, or the reduction in impacts (García-Díaz et al., 2021; Robertson et al., 2020). In some cases, the goal may be to locally eradicate an INNS from a region, possibly because at very low densities it produces massive impacts. In other contexts, the focus may be on preventing spread into a high priority conservation area, whereby containing the current invasive population is fundamental. While reducing the impact of an invasive population is a highly desirable outcome, for many INNS there are not enough data to identify impact-density thresholds to minimize INNS impacts. In such cases, managers can focus on reducing either the spread or the population size of the INNS. Management strategies should be evaluated against their effectiveness to achieve a specific objective. Ideally, a single management strategy would be identified as the best option to achieve various goals simultaneously. However, it is often the case that the cost of a particular management strategy can be prohibitively high (Nuñez et al., 2017), rendering it unfeasible. Therefore, an enduring question is whether the best management strategy to achieve containment of an invasive population of trees differs from the best strategy to reduce its population size, and from the best strategy to reduce its impact on the invaded ecosystem.

Critical biological invasion processes including spread, impact on recipient communities and compensatory responses to management take place at large spatial (landscape to regional) and long temporal (decades) scales, making them challenging both to manage effectively and to study in the field. This represents an obstacle for management programmes for invasive populations, as these need to be evidence-informed and maintained in the long term to be effective and achieve sustained gains (Mack et al., 2000). To carry out an experiment and assess the effectiveness of different management strategies would take decades for many invasive taxa. However, owing to time constraints, most experiments evaluate management of invasive species over very brief time scales (Kettenring & Adams, 2011). The use of simulation models can overcome these challenges and help gain insights into the long-term consequences of alternative management actions on invasive populations (Green et al., 2005). This is particularly useful when managing and researching invasive trees, which are long-lived and their invasive populations show long-term responses to management actions (Buckley et al., 2005; Caplat et al., 2014; Mason et al., 2021).

Among invasive trees, species from the *Pinus* genus stand out because of their massive use for forestry across the world (Essl et al., 2010), because of their high invasiveness (Nuñez et al., 2017; Simberloff et al., 2010) and because of their negative impacts on treeless ecosystems (Davis et al., 2019; Moyano et al., 2023; Pawson et al., 2010). Previous studies have identified three key variables for successfully managing *Pinus* invasions: (a) the timing when management actions begin (Mason et al., 2021); (b) the life stages targeted for control (Buckley et al., 2005); and (c) the selection of locations for control (Caplat et al., 2014). However, the role of these variables has generally been assessed in isolation, and against single management goals, such as reducing invasion spread (Buckley et al., 2005; Caplat et al., 2014), invasive population size (Brancatelli et al., 2024) or minimizing invasion impacts (Cuevas & Zalba, 2010). To design actionable management strategies, we need to consider how different management variables interact with each other, and how to best combine these management variables to achieve multiple goals (Mason et al., 2021). In this study, we assess how the interactions between delaying management actions, targeting different life stages for removal and prioritizing different locations for control in a landscape determine management effectiveness for one of the most invasive species within the *Pinus* genus, *Pinus contorta* (Rejmánek & Richardson, 1996, 2013; hereafter 'pine'). Furthermore, we evaluate management effectiveness considering three management objectives: (a) to reduce the spread of the invasive population, (b) to reduce its population size and (c) to reduce its impact on native grasslands in Patagonia (the southern end of South America, mostly covered by semi-arid native grasslands, which are progressively being replaced by non-native tree plantations and invasions).

We simulated a pine population spreading from a commercial plantation for 50 years, coupled with annual control actions which started either as soon as pines began to spread (when pines in the plantation become reproductive; proactive management) or assuming that control actions were delayed at incremental decadal intervals (reactive management). For control interventions, we targeted different life stages, prioritized areas at different locations of the landscape and explored a wide range of available budgets limiting the percentage of the landscape that could be managed every year. We aimed to answer the following set of comprehensive questions of management relevance: (1-a) Which is the minimum budget that achieves containment (sensu Robertson et al., 2020; i.e. only the area covered by the original commercial plantation is occupied by reproductive pines)? (1-b) Which strategy (combination of stage targeted and spatial prioritization) is effective with this minimum budget? (2-a) If we incrementally delay management, how much does the minimum budget necessary for containment increase? (2-b) Do the strategies that achieve containment with the lowest budget change if management is delayed? (3) Do the strategies that achieve containment also minimize the invasive population size and accumulated impact? (4) Which strategies achieve the most cost-effective reduction in invasion extent, invasive population size and invasion impact? (5) Which management variables best explain variation in management effectiveness (i.e. reduction in invasion extent, invasive population size and invasion impact)? We expected that targeting saplings in the invasion front would be most effective at containing the invasive population, because the survival rate of this stage has a strong influence on invasive population spread (Buckley et al., 2005; Caplat, Coutts, et al., 2012), and focusing management efforts on the periphery of the invasion is highly effective to slow down invasion spread (Caplat et al., 2014). Finally, we also expected that targeting adult trees would be more effective to reduce the impact of the invasive population because adults cause more damage than younger life stages (Franzese et al., 2017), while focusing control actions on areas with highest invasion density would reduce total population size in the long term.

2 | MATERIALS AND METHODS

To answer our research questions, we built a simulation model in a customized version of the modelling platform RangeShifter v2.0 (RS) (Bocedi et al., 2014, 2021). This Range Shifter model incorporates a module for management of invasive species and can simulate various dispersal kernels: negative exponential, double negative exponential, 2 Dt (suitable for modelling dispersal by animal vectors) and WALD (suitable for modelling dispersal by wind; Lambin et al., 2020). RS has been used to model biological invasions in the long term (Dominguez Almela et al., 2020, 2021; Plenderleith et al., 2022) and other ecological processes relevant to biological invasions, including dispersal (Ponchon et al., 2021) and range expansions (Fitt et al., 2019; Ponchon & Travis, 2022). Pines have been intensively studied, in terms of their demography (Brancatelli et al., 2022; Caplat, Coutts, et al., 2012; Wyse & Hulme, 2022), dispersal (Greene & Johnson, 1989; Wyse et al., 2019), spread (Buckley et al., 2005; Caplat, Nathan, et al., 2012; Wyse & Hulme, 2021) and impact (Moyano et al., 2023; Paritsis et al., 2018; Sapsford et al., 2022), which makes them an ideal study system to model invasions.

2.1 | Description of the individual-based spatially explicit model

We built an artificial landscape comprising two types of habitats: commercial pine plantation and native Patagonian grassland (Figure 1a). The complete landscape included 8 columns and 50 rows of square 25-m cells (allowing a small pine population in each cell), in total representing 25 ha, an area sufficiently large to integrate the full dispersal distance of pine seeds from the invasion front over 50 years. The southernmost single row represented the initial pine plantation because the majority of the seeds dispersed outside

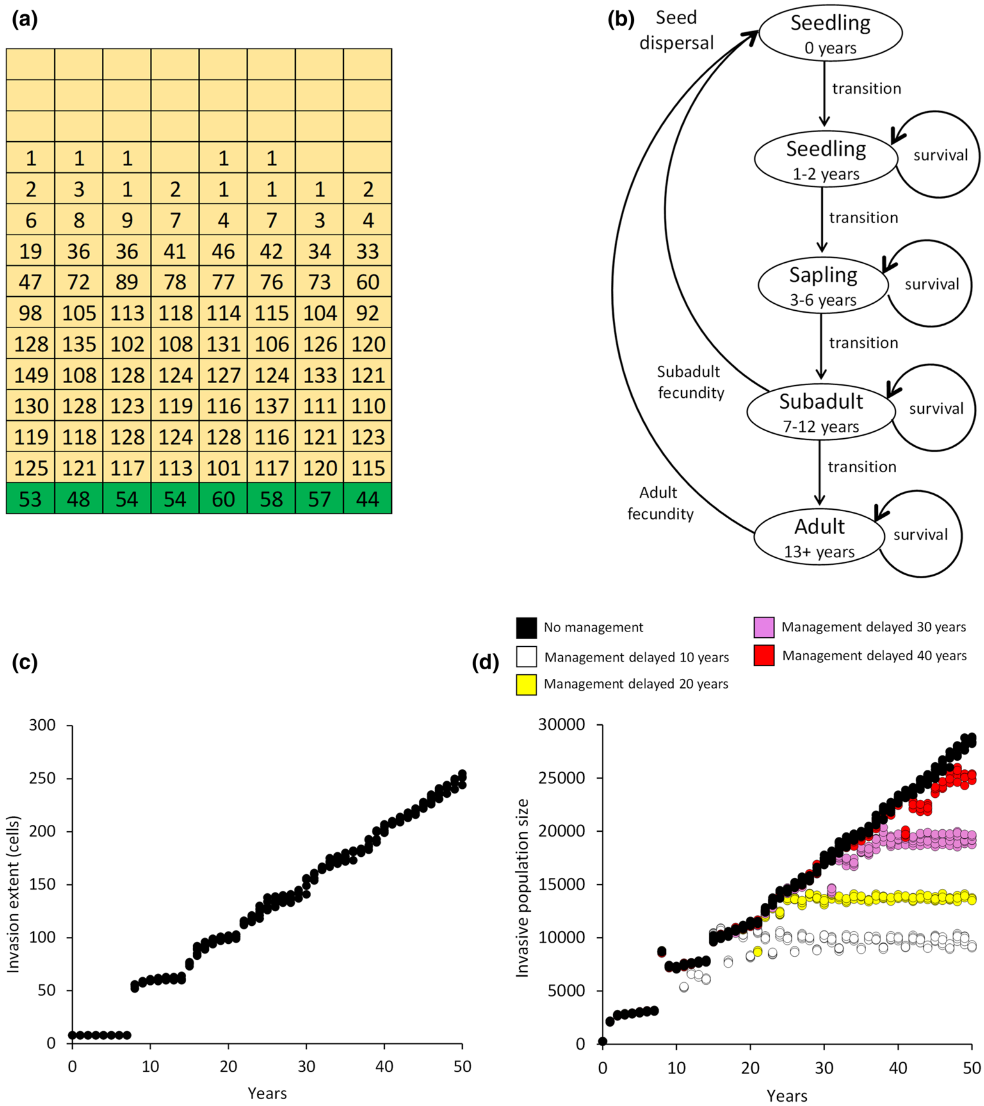

FIGURE 1 (a) Illustrative example of our modelled landscape with the bottom row of green cells representing the area of the initial commercial tree plantation and the rest of the cells representing the native grassland. Numbers indicate the number of pines (>0-year-old) per cell after 10 years without management. (b) Scheme representing our pine demographic model. (c) Plot based on data from a scenario without management, showing how invasion extent increases with time. (d) Plot based on data from an example, showing how the invasive population size increases with time during a simulation where management is delayed in 10 year intervals (including the scenarios represented in (a and c)).

a plantation come from the trees at the edge. The rest of the cells represented native grasslands. Pines were initially present only in cells representing the plantation, at a density of 33 subadult pines/cell (528 pines/ha) in all simulations, which lies within the range for pine plantations in Patagonia. The prevailing wind direction in the model was from South to North, emulating the dominance of a single (westerly) wind direction as it occurs throughout Patagonia. We implemented a female-only stage structured matrix model in RS, representing a hermaphrodite plant species. The life cycle was represented by five stages (as required in a RS model for a long-lived species; Table 1, Figure 1b). Emigration, the movement of individuals across the landscape—in this case the dispersal of seeds—and settlement, recruitment of individuals in a specific location of the landscape—here the establishment of seedlings in a specific cell—were

TABLE 1 Stages and their corresponding age, height, and fecundity ranges for our pine model.

Stage	Age (years)	Height (cm)	Fecundity
Seedling (<1 year)	0	Up to 15	None
Seedling (>1 year)	1–2	15–51	None
Sapling	3–6	51–219	None
Subadult	7–12	219–491	Low (~9 seedlings/year)
Adult	13 and over	491 and over	High (~149 seedlings/year)

Note: For fecundity values, we refer to seedlings instead of seeds because we simulated the dispersal of established seedlings—rather than seeds—to reduce computational efforts (Appendix S1).

density-independent. We used the WALD kernel as the transfer model because it predicts long distance dispersal by wind more accurately than other analytical mechanistic models (Katul et al., 2005). Each time step in the model represented 1 year.

2.2 | Demographic and dispersal parameters

We estimated parameters of the demographic and dispersal components of the RS model using approximate Bayesian computation (ABC) from field data recorded at Coyhaique Alto (45°30′ S; 71°42′ W; Aysén Region, Chilean Patagonia) where *Pinus contorta* is invading the native grasslands from an adjacent commercial plantation (Langdon et al., 2010; Pauchard et al., 2016; Appendix S1). For this fieldwork we did not require permits or licences.

2.3 | Sensitivity analyses

To assess the effect of parameter variations on our RS model outputs, we carried out sensitivity analyses. The subset of parameters we included were those 10 parameters for which estimation by ABC was least informative (i.e. highest overlap between the prior and the posterior distributions; Figure S3; Appendix S1).

2.4 | Simulation experiments

To answer our research questions, we conducted virtual experiments applying a fully factorial design, whereby we ran five replicates of all the combinations of levels of the variables 'management delay', 'stage targeted', 'control location' and 'total budget' (Table 2). We simulated a pine population for 50 years, starting from a 7-year-old plantation (already producing seeds), adjacent to a native grassland. Management actions took place exclusively in the grassland, since the original plantation (southernmost eight cells) was assumed to be grown for commercial purposes. We simulated delayed control actions at 0, 10, 20, 30 or 40 years (from the moment pines started spreading, when the pines from the plantation become reproductive) to assess the consequences of delaying management. These incremental delays were based on real-world scenarios where pine invasive populations have been spreading for one to four decades without management. Once control actions started, they were carried out annually. We targeted different life stages for control: seedlings (1–2-year-old pines), saplings (3–6 years), subadults (7–12 years), adults (13 years or more) or all four stages (see Table 1 for a detailed description of the life stages). In scenarios where all life stages were removed simultaneously, different stages were selected at random until all trees were removed, or the available budget was spent. We selected cells for control actions at different locations of the landscape, according to different prioritization criteria (hereafter control location): (1) The random criterion selects occupied cells for management arbitrarily across the landscape. (2) The invasion front criterion prioritizes recently colonized cells. (3) The pine density criterion prioritizes cells with the highest population size of the targeted stage(s). (4) The impact criterion prioritizes cells which have higher accumulated impact on native grassland productivity. To quantify this impact of pine invasion on grassland productivity, we built density impact curves relating the effect of increasing pine density (for each pine stage) on native grassland productivity (Figure S1), based on data obtained from *P. contorta* invasions in native grasslands in Northwest Patagonia, Argentina (Moyano et al., 2023). These curves were fitted using an asymptotic function, with one single parameter (beta), which we included in our sensitivity analyses (Appendix S1).

We also modified the total available budget, which limits the area of the landscape that can be managed each year (see below), to identify the minimum budget that achieves containment. To do so, first we explored a range of budgets, from 0 US$/year to 10,000 US$/year, in increments of 500 US$/year to find approximate levels of investment sufficient to contain the invasive population for each level of management delay (which we expected to increase management costs). Once we identified these (e.g. 500 US$/year was enough for containment with no management delay), we reduced them in intervals of 100$/year to find a more precise minimum containment budget (e.g. 200 US$/year was the minimum budget that contained the invasive pines if management was not delayed).

We calculated management extent (i.e. the number of cells that could be managed every year) based on the cost of mechanical control actions, 2023 US$, of invasive *P. contorta* populations in National Reserve Malalcahuello, Chilean Patagonia (Naour et al., 2016). From experimental management plots, we obtained the total labour cost of removing individual pines of each stage. We carried out a simulated experiment in RS without management to obtain average densities for each pine stage across the invaded landscape in the absence of management. We used these densities to calculate an

TABLE 2 Summary of our experimental design.

Effect	No. of levels	Values
Management delay	5	0, 10, 20, 30, 40 years
Stage targeted	5	All four stages (S1–S4) Seedlings (S1, 1–2 years), Saplings (S2, 3–6 years), Subadults (S3, 7–12 years), Adults (S4, 13 years or more)
Control location	4	Random, Invasion front, Impact on grassland productivity, Pine density
Total budget	36	0 to 10,000 US$/year in increments of 500 US$/year and additional levels around minimum containment budgets
Simulation replicates	5	
Total simulations	18,000	

Note: We conducted a full factorial experiment in which we ran five replicates of all the combinations of levels of the variables 'management delay', 'stage targeted', 'control location' and 'total budget'.

average cost per managed cell. For example, to calculate the average cost of removing all adults from a cell, we multiplied the cost of removing each adult by the average number of adults per cell. By dividing the total budget (US$/year) by the cost of removing pines in each cell, we obtained the total number of cells that could be managed per year. These values ranged from 1% to 100% of the invaded area, depending on the targeted stage(s) and the available budget (Figure S2). Smaller pine stages are more difficult to find in the field, and therefore, we assigned an increasing probability of detection to each pine stage, with their corresponding removal percentage. As a result, we assumed that, for each cell selected for management, control actions effectively removed 80% of seedlings (i.e. 20% of seedlings were missed because of their small size), 90% of saplings, and 99% of both subadults and adults.

Annual control actions were applied before dispersal. We assumed that local population size was imperfectly known by drawing values from a normal distribution centred on the true count and specifying a coefficient of variation of 5%. To assess whether increasing this coefficient of variation in detected population size affected our response variables, we increased it to 7.5% and 10% and evaluated the proportion of variability in our response variables explained by these changes. Each simulation was replicated five times. By the end of each simulation (Year 50), we calculated three response variables: Pine invasion extent (the total number of grassland cells occupied by reproductive pines; Figure 1a,c), invasive pine population size (the total number of pines of age >0 years across the grassland; Figure 1a,d) and pine invasion impact on grassland productivity (the accumulated impact of pine invasion on native grassland productivity across the landscape).

2.5 | Data analyses

To identify the minimum budget that achieves containment without management delay (Question #1a), we evaluated the invasion extent by the end of our simulations (i.e. 50 years) for every management strategy. Only if a management strategy consistently showed an invasion extent of eight cells (i.e. those cells originally occupied by the pine plantation) occupied by reproductive pines did we confirm this scenario as full containment, at the corresponding budget. The lowest budget with such a scenario was the minimum containment budget. To identify which strategy is effective with this minimum containment budget (Question #1b), we evaluated which combinations of stage targeted and control location (without management delay) contained the invasive population (invasion extent = 8 cells) with this minimum budget.

To assess how the minimum containment budget increases as we delay management (Question #2a), we used the range of available budgets (from 0 US$/year to 10,000 US$/year) and identified the minimum containment budget (the minimum budget level with which full containment of the invasive population can be achieved) for each level of management delay (0, 10, 20, 30 and 40 years). Lastly, to evaluate whether the management strategies that are effective with the minimum containment budget change when we delay the start of management (Question #2b) we identified the combinations of stage targeted and control location that achieved full containment with these minimum containment budgets and compared them across levels of management delay.

To assess whether the most effective strategy for containment is also the most effective at reducing the invasive population size and accumulated invasion impact (Question #3), we ranked all strategies (total of 720 strategies for each of the five levels of management delay). For each delay level, we ordered management strategies according to the mean invasion extent, mean invasive pine population size and mean invasion impact, to find which strategies were most effective at reducing these by the end of the simulations (Year 50) relative to our simulations without management. We also ranked strategies for each delay level, according to the variance of these response variables (invasion extent, invasive pine population size and invasion impact) to identify which strategies are more likely produce consistent results, which is highly desirable for managers.

To assess how the targeted pine stage affects control actions effectiveness, we built three regression models. For each of these regression models, the predictive variable was pine stage selected for control, and the response variables were pine invasion extent, population size and impact on native grassland productivity, respectively. In the case of invasion extent and invasive population size, we assumed a negative binomial error distribution (because for both response variables model residuals showed overdispersion) ('glm.nb' function from the 'MASS' package, Venables & Ripley, 2002). For invasion impact, we assumed a normal error distribution (lm function in R; Chambers & Hastie, 1992; Wilkinson & Rogers, 1973). To evaluate the effect of criteria of spatial prioritization on management efficacy, we built regression models with the same response variables as above but using control location (described above) as the predictive variable. We evaluated the effect of different factors (targeted stage and control location) on management strategy effectiveness (invasion extent, invasive population size and invasion impact) using estimated marginal means analyses ('emmeans' function, Lenth, 2020). Estimated marginal means are obtained by using a model to make predictions (in our case of invasion extent, invasive population size or invasion impact) over a regular grid of predictors combinations. These predictions can be averaged across one or more predictors (in our case, targeted stage or control location) to make pairwise comparisons.

To identify which strategies achieve the most cost-effective reduction in invasion extent, invasive population size and invasion impact (Question #4), we ranked strategies for each delay level according to the reduction in invasive population size, invasion extent and invasion impact (using the scenarios without management as a reference) per 1000 US$ spent on management. For example, in the case of invasive population size, the reduction in this response variable was obtained by subtracting the population size of the managed scenario from the population size of the unmanaged scenario; then, this reduction was divided by the total budget of that particular management scenario (divided by 1000). For each year, we calculated the present value (PV) of the management budget as:

$$PV = \frac{\text{Budget}}{(1+r)^t}$$

where Budget is the total cost of the management strategy (using dollars from 2023), r is the discount rate (here we used three values, 3%, 5% and 10%), and t is the year since the start of the invasion (White et al., 2022). For each strategy, we calculated the total management budget through the sum of the present value of the management budget of each year there was management. We also ranked strategies for each delay level, according to the variance of the reduction in the response variables per 1000 dollars spent in management, calculated using the present value formula, to evaluate which strategies obtained more consistent results.

To evaluate which management variables best explain variation in management effectiveness (Question #5), we built statistical models, through which we assessed how much variability in our three response variables (invasion extent, invasive population size and invasion impact) was explained by each of the treatments (management delay, targeted stage, control location and available budget) included in our management strategies. To assess how variation in invasion extent and variation in invasive population size were explained by different treatments, we built regressions with a negative binomial error distribution ('glm.nb' function from the 'MASS' package, Venables & Ripley, 2002). To calculate the proportion of deviance explained by each predictive variable, we sequentially removed each variable (one at a time) from our regression models and assessed the differences in deviance explained. For example, when we removed targeted stage from our regression model with invasion extent as response variable, the proportion of deviance explained by the model was reduced by 25%; therefore, this predictive variable accounted for 0.25 of the total deviance in invasion extent. To assess the distribution of variability in invasion impact among treatments, we built linear models having a normal error distribution (lm function in R; Chambers & Hastie, 1992; Wilkinson & Rogers, 1973). Similar to the proportion of deviance, to calculate the proportion of variance explained by each predictive variable we sequentially removed each variable (one at a time) from our regression models and assessed the differences in variance explained. For example, when we removed targeted stage from our regression model with invasion impact as response variable, the proportion of variance explained by the model was reduced by 29%; therefore, this predictive variable accounted for 0.29 of the total variance in invasion impact.

To evaluate the proportion of variability in our response variables accounted by changes in the coefficient of variation (c.v.) in the detected population size, we assessed the proportion of deviance in invasion extent and invasive population size, as well as the proportion of variance in invasion impact explained by variations in the c.v. of detected population size. We re-ran management scenarios using three levels of c.v. (5%, 7.5% and 10%), all levels of life stage targeted (seedlings, saplings, subadults, adults or all stages), one fixed level of control location (prioritizing cells with high density), all levels of management delay (0, 10, 20, 30 or 40 years), and three contrasting budget levels (200, 3500 and 7500 US$/year). Since changes in the c.v. in detected population size could only affect the RS model predictions if the option to select cells weighted by local population size is applied, we set the control location variable fixed in the criterion which prioritizes cells with high pine density. With the results from these simulations, we calculated the proportion of deviance in invasion extent and invasive population size, as well as the proportion of variance in invasion impact explained by variations in the c.v. of detected population size as explained in the previous paragraph.

In the case of the general linear models, we tested models for normality of residuals by analysing the distribution of residuals visually. To check homogeneity of variance, we evaluated that there was no pattern between model residuals and fitted values (Quinn & Keough, 2002). Furthermore, none of our data points showed a Cook's distance over 1, which indicates the absence of high leverage points (Cook & Weisberg, 1982). We conducted all analyses using R v.4.1.1 (R Development Core Team, 2021).

3 | RESULTS

3.1 | Model parameterization and sensitivity analyses

The posterior distributions of 11 RS parameters were refined substantially through ABC estimation, whereas for 10 parameters, the posterior distribution varied little from the prior (i.e. the field data were uninformative for them) (Figure S3). Notably, the density dependence coefficient, $1/b$, was found to be substantially higher than the prior estimate. The effects of competition between seedlings and saplings on the survival of saplings were estimated to be very low, whereas the estimated effects of subadult trees on saplings were lower than our prior estimates (such that subadult trees have only roughly half the effect of adult trees). In general, the parameters of the WALD dispersal model were altered little by the data, other than the mean wind direction, which was estimated to lie in a narrower range for the field site.

Among the parameters included on our sensitivity analyses, we found that invasion extent was most sensitive to the dispersal parameters seed terminal velocity, adult seed release height and the standard deviation of vertical wind speed (Figure S8a). On the contrary, invasive population size was most influenced by the demographic parameter sapling weight for density dependence in survival of seedlings under 1 year old (i.e. the effect of saplings on seedlings survival; Figure S8b). Similar to invasion extent, invasion impact was most sensitive to seed terminal velocity and adult seed release height (Figure S8c).

3.2 | Containment of pine invasions

We found that the minimum budget that achieved full containment of the invasive population, without management delay, was 200 US$/year (Question #1a). With this minimum budget, containment was achieved by targeting saplings (Figure 2A), selecting cells for management either randomly, prioritizing those in the invasion

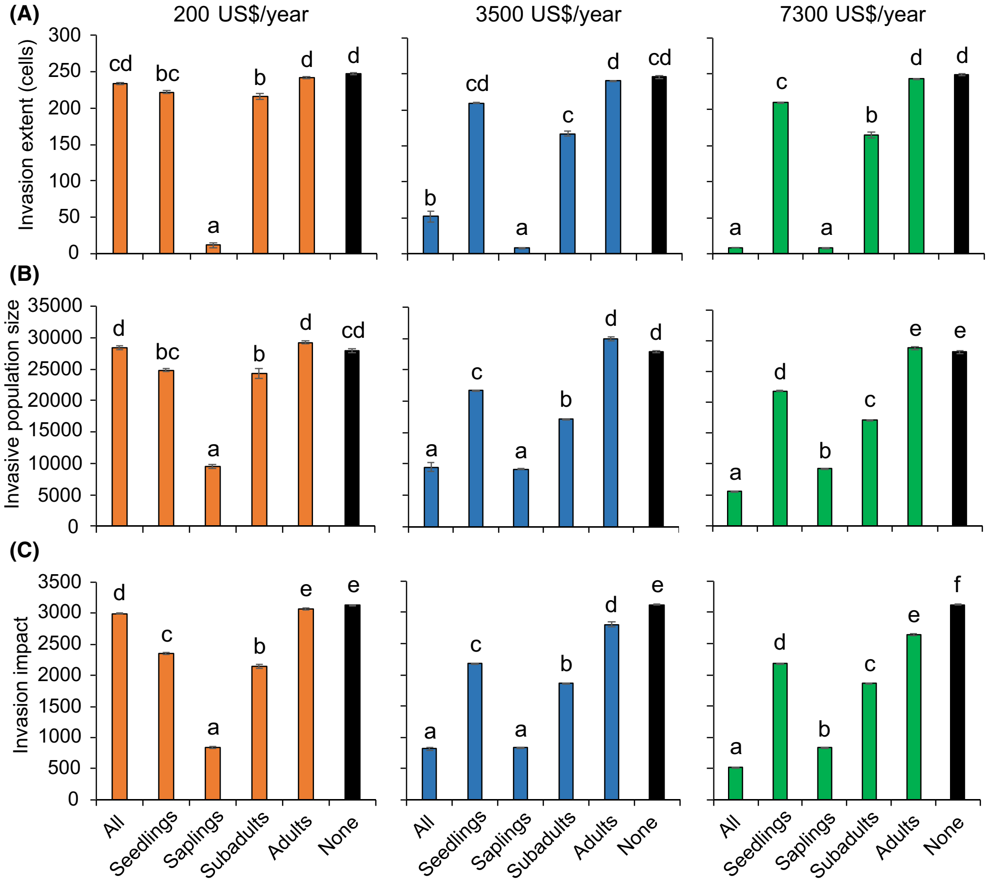

FIGURE 2 Mean (+/− SE) of (A) invasion extent, (B) invasive population size and (C) invasion accumulated impact by Year 50, for management strategies without delay targeting different pine stages, and contrasting available budgets that achieve containment. 200 US$/year achieves containment by targeting saplings, 3500 US$/year achieves containment by targeting all stages with 10 years of management delay, and 7300 US$/year achieves containment by targeting all stages even with 40 years of management delay. Different letters indicate significant differences ($p < 0.05$; Tukey method) among stages within the same budget. The scenario with no management is represented by black bars.

front, or those with the highest impact (Figure S5a) (Question #1b). Effectiveness progressively decreased when focusing control actions only on subadults, seedlings and adults, in that order (Figure 2A). In fact, there was no significant difference in invasion extent between no management and removing only adults. There was no apparent advantage of focusing management efforts on different parts of the landscape (i.e. control location; Figure S4a). All spatial prioritization criteria seemed equally effective at reducing invasion extent, when management was not delayed (Figure S5a).

As management was delayed, the minimum annual budget that achieved containment increased to 3500, 4000, 5200 and 7300 US$/year for delays of 10, 20, 30 and 40 years, respectively (Table S5; Question #2a). As management delay increased, the number of strategies that achieved containment decreased: 184, 74, 64, 48 and 19 strategies (out of a maximum of 720 strategies) achieved containment for delays of 0, 10, 20, 30 and 40 years, respectively (Table S6; Question #2b). For instance, if management was not started immediately after pines start spreading (Year 0), containment was only achieved by targeting all stages. In addition, containment was achieved with 200 US$/year by targeting only saplings in scenarios without management delay. With delays of 10 and 20 years, containment was achieved with 3500 and 4000 US$/year, respectively, but only if all stages were targeted selecting cells for management randomly. Likewise, with delays of 30 and 40 years, containment was achieved with 5200 and 7300 US$/year, respectively, but only if all stages were targeted at cells in the invasion front (with other control locations the annual cost of containment increased). All these strategies consistently achieved full containment, showing no variability across replicates.

Delaying control actions strongly reduced the effectiveness of the management strategies that achieved containment when started early (Figure 3a). With the minimum budget that achieved containment without management delay (200 US$/year), targeting saplings was more effective to reduce invasion extent than targeting all stages, across all management delays. However, delaying management actions strongly reduced the advantage of targeting saplings. With the budget that achieved containment if management was delayed 10 years (3500 US$/year), targeting saplings was more effective to reduce invasion extent for a rapid response (i.e. no delay). However, targeting all stages became more effective as

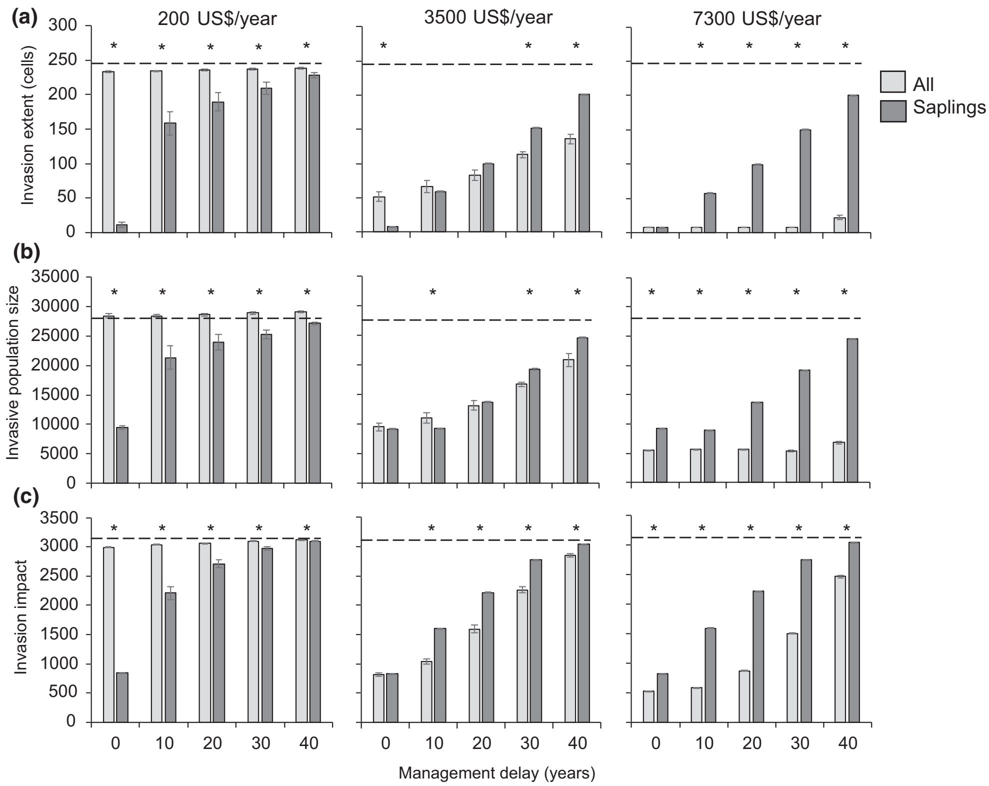

FIGURE 3 Mean (+/− SE) of (a) invasion extent, (b) invasive population size and (c) invasion accumulated impact by Year 50, for management strategies targeting all pine stages (light grey) or saplings (dark grey), with different levels of management delay, and contrasting available budgets that achieve containment. Here, to explore the widest variation in management effectiveness, we focused on the targeted stages with highest containment effectiveness (saplings and all stages). 200 US$/year achieves containment by targeting saplings with no management delay, 3500 US$/year achieves containment by targeting all stages with 10 years of management delay, and 7300 US$/year achieves containment by targeting all stages even with 40 years of management delay. An asterisk (*) indicates significant differences ($p < 0.05$; Tukey method) between stages targeted within the same budget and the same management delay. The scenario with no management is represented by the dotted horizontal line.

management delay increased. With a high enough budget, containment could be achieved even after 40 years of management delay (7300 US$/year), and targeting all stages was more effective to reduce invasion extent across all management delays. Furthermore, if management was delayed, complete containment was only achieved through control of all pine stages (Figure 3a), resulting in increased costs (Figure S2). As management was delayed, some control locations became more effective than others (Figures S5a–S7a). For instance, with the minimum containment budget (200 US$/year), selecting areas for control of saplings in the invasion front achieved the highest reduction in invasion extent when management was delayed (Figure S5a). Control efforts on the invasion front seemed more effective to achieve containment when management was delayed 30 years or more (Table S6).

3.3 | Reducing the invasive population size and impact

With the minimum budget that achieved full containment of the invasive population without management delay (200 US$/year), targeting saplings was also the most effective strategy to minimize the invasive population size (Figure 2B, Table S8) and its accumulated impact regardless of the sites selected for control (Figure 2C, Table S10; Question #3). Across levels of management delay and available budgets, the 10 strategies that were most effective at reducing invasive population size, invariably targeted all pine stages with budgets of at least 4000–5200 US$/year if management was delayed up to 30 years, and at least 7500 US$/year if management was delayed 40 years (Table S8). These strategies included different spatial prioritization criteria, with the invasion front criterion increasing in frequency from 0% without management delay to 80% with 30 years of management delay and dropping to 30% with 40 years of management delay. All these strategies, in addition to being the most effective at reducing invasive population size, achieved full containment of the invasive population. The 10 strategies with the lowest variance in invasive population size across levels of management delay, included all possible levels for every management variable, showing no clear pattern in strategies with lower variability (Table S9).

The 10 strategies that were most effective at reducing invasion impact, across different levels of management delay and available budgets, always targeted all pine stages, with budgets of at least

5000 US$/year if management was delayed up to 10 years, and at least 7300–7400 US$/year if management was delayed 20 years or more (Table S10). Most of these strategies (92.5%) also achieved full containment of the invasive population. These strategies focused control actions on different areas of the landscape, increasingly prioritizing areas of higher impact as management delay increased: 10%, 50%, 20%, 70% and 80% of these best strategies focused on areas of higher impact with levels of management delay of 0, 10, 20, 30 and 40 years, respectively. Furthermore, the 10 strategies with the lowest variance in accumulated impact targeted all stages (50%) or saplings (50%) if management was not delayed, targeted all stages with delays of 10 and 20 years, and targeted different pine stages (except for saplings) if management was delayed 30 or 40 years (Table S11). The cost of these strategies with lowest variance in impact was 7200 US$/year or higher when targeting all stages, and highly variable when targeting each stage individually.

3.4 | Cost-effective reduction in pine invasion

The 10 strategies that achieved the highest reduction in invasion extent and invasive population size per dollar invested (assuming a 5% discount rate), across different levels of management delay, mostly targeted only saplings (100% of strategies for invasion extent and 90% for invasive population size; Table 3a,b, Tables S12 and S14; Question #4). The 10 strategies that achieved the highest reduction in invasion impact per dollar invested targeted only saplings if management was not delayed, with increasing frequency of other pine stages targeted as management delay increases: 40%, 60%, 70% and 80% for management delays of 10, 20, 30 and 40 years, respectively (Table 3c, Table S16). The strategies that were most effective at reducing invasion extent, invasive population size and invasion impact per dollar invested, across all levels of management delay, invested 500 US$/year or less, using all different spatial prioritization criteria. The 10 strategies with the lowest variance in invasion extent, population size and impact reduction per dollar invested, across all levels of management delay, targeted nearly all pine stage options, with average budgets of 7680–8950 US$/year for invasion extent, 8890–10,000 US$/year for invasive population size, and 6550–9200 US$/year for invasion impact (Tables S13, S15 and S17), and using all different spatial prioritization criteria. When assuming a 3% (Tables S18–S23) or 10% discount rate (Tables S24–S29), we obtained very similar results in the rankings of strategies.

3.5 | Drivers of pine invasions

Variation in invasion extent and invasive population size after 50 years were mostly explained by the pine stage targeted for control actions, accounting for 25% and 30% deviance, respectively (Table S30; Question #5). Management delay and available budget accounted for between 6% and 12% of deviance in invasion extent and invasive population size, while control location only accounted for up to 0.3%. In the case of accumulated invasion impact, the most influential variable was management delay (accounting for 35% variance), but closely followed by targeted stage (29% variance), then available budget (5% variance) and control location (0.1% variance).

TABLE 3 Management strategies ranked according to (a) highest reduction of invasion extent per 1000 dollars invested, (b) highest reduction of invasive population size per 1000 dollars invested and (c) highest reduction of invasion impact per 1000 dollars invested (assuming a 5% discount rate) for scenarios without management delay.

(a)

Rank	Stage	Location	Delay	Budget	Inv. extent (cells) reduction/1000US$
1	Sapling	inv. front	0	100	63
2	Sapling	random	0	200	63
3	Sapling	inv. front	0	200	63
4	Sapling	impact	0	200	63
5	Sapling	density	0	200	59
6	Sapling	random	0	300	41
7	Sapling	inv. front	0	300	41
8	Sapling	impact	0	300	41
9	Sapling	density	0	300	41
10	Sapling	random	0	100	35

(b)

Rank	Stage	Location	Delay	Budget	Population size reduction/1000US$
1	Sapling	inv. front	0	100	6657
2	Sapling	inv. front	0	200	4928
3	Sapling	impact	0	200	4917
4	Sapling	random	0	200	4877
5	Sapling	density	0	200	4532
6	Sapling	inv. front	0	300	3248
7	Sapling	density	0	300	3219
8	Sapling	random	0	300	3217
9	Sapling	impact	0	300	3214
10	Sapling	random	0	100	2561

(c)

Rank	Stage	Location	Delay	Budget	Impact reduction/1000US$
1	Sapling	random	0	100	626
2	Sapling	impact	0	200	599
3	Sapling	inv. front	0	100	599
4	Sapling	inv. front	0	200	599
5	Sapling	random	0	200	599
6	Sapling	density	0	200	589
7	Sapling	density	0	300	395
8	Sapling	inv. front	0	300	395
9	Sapling	impact	0	300	395
10	Sapling	random	0	300	395

Changes in the coefficient of variation in the detected population size (5%, 7.5% and 10%) accounted for a negligible fraction of the deviance in invasion extent, the deviance in invasive population size, and the variance in invasion impact (<0.001% in all cases; Table S31), indicating that our arbitrary choice of 5% c.v. in the main set of experiments had no bearing on the results.

4 | DISCUSSION

Our results show that, if management is not delayed, targeting saplings is the most effective strategy to contain the invasion at the lowest management cost possible (200 US$/year) and also the most effective strategy to minimize invasive pine population size and impact. However, if management is delayed, the budget required to contain the invasive population increases substantially (from 1650% to 3550% for delays of 10 and 40 years, respectively) and targeting all stages becomes more effective at reducing invasion extent, invasive population size and invasion impact. On the contrary, across all levels of management delay, the most cost-effective reduction in invasion extent and invasive population size is achieved by removing saplings, while for invasion impact this is only the case if management is not delayed. Overall, our results show that the pine stage to target is the most influential management variable on pine invasion extent and population size, whereas management delay (from the moment pines start spreading) shows a stronger effect on invasion impact on native grassland productivity, although which stage to remove remains highly influential. Nevertheless, the interaction between management delay, targeted pine stage and location of control actions must be considered for each particular scenario.

Targeting saplings early in the invasion process is the key to effective reduction in invasive pine spread, population size and impact with the lowest possible budget. Our results are in accordance with previous studies, which found that early removal of pine invasions is more cost-effective (Mason et al., 2021), and that pine sapling survival has a strong influence on invasive pine population spread (Buckley et al., 2005; Caplat, Coutts, et al., 2012). One of the main advantages of targeting saplings early is that their removal involves a low cost and, therefore, control actions can be implemented across the whole invaded landscape with most budget levels evaluated here. However, our main contribution is to show how the interaction between delaying management actions, targeting different life stages for removal and prioritizing areas for control actions at different locations of the landscape shapes management effectiveness. Controlling saplings without delay prevents invasive pines from becoming reproductive, which is essential to reduce seed dispersal, a major driver of population spread (Clark et al., 1998; Coutts et al., 2011; Davies & Sheley, 2007; Jongejans et al., 2008). The removal of pines before their reproductive stage also reduces propagule pressure, a key driver of establishment success (Blackburn et al., 2015; Simberloff, 2009). Complementarily, adults are major contributors to the impact of pine invasions (Franzese et al., 2017), so preventing saplings from becoming adults contributes to reducing potential damage in the long-run. However, the advantage of targeting saplings decreases with management delay. As management is delayed, an increasingly larger area becomes occupied by all pine stages, as seeds are dispersed from the plantation, seedlings emerge, turn into saplings, then subadults and adults. As a result, if control actions only target saplings, the other pine stages will not be removed and will continue to contribute to population growth, spread and impact, turning this strategy ineffective. Therefore, if management is delayed, it becomes key to target all pine stages and to invest a much higher budget to achieve full containment of the invasive population within the area of the original plantation.

While a high enough budget can secure invasive population containment and the reduction in the invasive population size even if management is delayed for several decades, the accumulated impact caused throughout the years without management cannot be undone solely by removing the invasive population from the invaded grassland (as evidenced by high impact levels even when pines were removed completely, Sapsford & Dickie, 2023). As a result, the impact produced by this invasive population on native grasslands strongly increases with each decade that management is delayed, and starting control actions early becomes key. Therefore, management of an invasive population should start as early as possible to minimize the damage caused to the invaded ecosystem (Ahmed et al., 2022).

Interestingly, while targeting adults (and subadults) intuitively seems a very good option and is usually recommended as the most effective way to reduce propagule pressure in the landscape, this strategy was ineffective throughout all our scenarios. While removing all invading adults and subadults across the landscape should reduce the spread rate of the invasive population, once individuals become subadults or adults it becomes extremely difficult to remove all of them. First, to focus management efforts on subadults and adults, we need to wait 7 and 13 years, respectively, to allow seedlings to become saplings, then subadults and adults. This is an unnecessary delay allowing for a build-up in the number of seedlings and saplings, which soon become subadults and adults. In addition, it is much more expensive to control subadults and adults than to control seedlings and saplings, which strongly limits the management extent when targeting the former. Usually, the goal of removing adults and subadults is to prevent their production and dispersal of seeds, to prevent further pine spread. However, when targeting either adults or subadults (but not both), the remaining reproductive stage will still produce and disperse seeds. Nevertheless, controlling only adults and subadults may be relevant for long-term invasions in larger landscapes, where the dispersal range of seeds from the original plantations is limited.

Unexpectedly, the location of control actions did not consistently change management effectiveness, although in some cases, we found benefits from prioritizing certain areas for control. One possible explanation is that we separated the effects of targeting different life stages from the effects of prioritizing different areas of the landscape for control. While Caplat et al. (2014) found that focusing management efforts on the invasion front was consistently more effective to contain the invasive pine population, they removed all pines from each managed cell, without considering different life stages. It is possible that by focusing on cells further from the seed source, they removed a higher proportion of younger life stages, such as seedlings and saplings. Therefore, they may have found that the invasion front is a management priority, but only because it includes a higher proportion of saplings. By targeting different life stages, we have separated the effect of spatial prioritization from the proportion of different life stages across the landscape.

Future research should involve testing specific short-term predictions from our models. For instance, it would be possible to measure in the field, 1 year after management actions took place, the effect of our best management strategies on invasive pine densities across a range of distances from commercial pine plantations. This way, we suggest building an adaptive management scheme, where the best management strategies from our simulation experiments are implemented on pine invasive populations in the field. Over a few years, their effectiveness is monitored based on short-term specific predictions, providing data to evaluate them and generate alternative, improved strategies. These new strategies are then tested in simulated experiments, and those with the best results are again implemented in the field, in an iterative cycle that progressively improves management of invasive pine populations (Dietze et al., 2018). A first step in this iterative process is the collection of more field data to inform our model parameters with highest influence on our response variables, as shown by our sensitivity analyses. These include both dispersal parameters (seed terminal velocity, adult seed release height and the standard deviation of wind speed) and demographic parameters (the effect of sapling competition on seedling survival). We note that our field data were collected long before the development of the model, and thus not with the estimation of model parameters in mind. In order to improve estimation by ABC of WALD model parameters, and hence prediction of invasion extent and impact, accurate and precise prior estimates of seed terminal velocity are required, and field plots should be spread widely over the area of potential invasion (including beyond the invasion front if invasion has already commenced).

We acknowledge that our study has some limitations for transferring to real-world situations. First, to focus on broad patterns we built a very simple landscape with only one commercial pine plantation, but many landscapes include multiple commercial plantations. However, most seed dispersal that contributes to an invasive population comes from the single closest plantation. Second, since this was not our goal, we did not focus on methods of control (i.e. mechanical, burning, chemical), but this may be relevant when focusing on sparse vs. dense invasive pine populations, or when considering differences among regions of the world where pines are invasive (Nuñez et al., 2017). Furthermore, different methods may have different management costs per unit of area. For some removal methods, the cost of removing individuals at different life stages may not differ as much as for the mechanical method, which could reduce the advantages of targeting saplings. In addition, not all methods can be applied for the removal of specific life stages. Chemical control through airborne interventions or control through burning makes it impossible to select different stages for removal. On the contrary, choosing which stage to remove is feasible with mechanical and chemical control interventions on the ground, control methods for which our results can be applied. Third, for invaded landscapes where the original pine plantations have been removed, the most effective strategy to reduce the spread and impact of an invasive population may involve removing all reproductive individuals (since these are the only seed sources). Fourth, since we did not consider scenarios where different pine stages were simultaneously managed at different locations of the landscape, there could be an interaction between life stage and control location not captured in our experiments. Nevertheless, these caveats and limitations can be addressed and refined via the iterative improving process described above. Therefore, the management recommendations we formulated based on our results can be applied in the field by managers, and eventually, these recommendations can be improved as new field data become available.

In this study, we found that targeting saplings early is the most effective way to slow down pine spread and reduce its population size and impact, investing management resources in the most efficient way. However, when management is delayed, there is a need to appeal to decision criteria. Managers can either invest a lot of resources to remove all pines (targeting all stages) from the invaded area, or they can consider that the recovery of the invaded area is unfeasible (e.g. if resources are scarce), and focus limited resources on preventing further spread (targeting only saplings; Caplat, Coutts, et al., 2012; Evans et al., 2011). These results can be applied to guide management of invasive woody species, across different contexts. In the same scenario where we gathered the field data with which we derived our model parameters (i.e. *P. contorta* invasions in Patagonian grasslands both in Chile and Argentina), managers could directly use our results to guide invasive pines removal. Alternatively, our RS model could be adapted to new landscapes and timeframes by adjusting the relevant parameters while keeping the same demographic and dispersal parameter values that we have used here. Our study can be replicated to guide the management of any invasive woody species where enough data are available to parametrize the simulation models. For species that currently lack sufficient data, acquiring the information that can be used for this type of modelling is a first step. Here, we show the necessary data for estimating the appropriate modelling parameters, hoping to trigger more research on this topic, which will help make management of invasive species more efficient.

AUTHOR CONTRIBUTIONS

Jaime Moyano, Xavier Lambin and Martin A. Nuñez conceived the ideas and designed the methodology. Barbara Langdon, Aníbal Pauchard and Jaime Moyano collected the field data. Jaime Moyano and Stephen C. F. Palmer designed and carried out the management simulations. Jaime Moyano, Pablo García-Díaz, Stephen C. F. Palmer and Paul Caplat analysed the data. Jaime Moyano and Pablo

García-Díaz led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Barbara Langdon is an associate editor of *Journal of Applied Ecology* and Martin Nuñez is a senior editor of *Journal of Applied Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.wstqjq2x3 (Moyano, García-Díaz, et al., 2024).

ORCID

Jaime Moyano https://orcid.org/0000-0002-7072-0527
Pablo García-Díaz https://orcid.org/0000-0001-5402-0611
Barbara Langdon https://orcid.org/0000-0001-8397-1774
Paul Caplat https://orcid.org/0000-0002-2449-3079
Xavier Lambin https://orcid.org/0000-0003-4643-2653
Aníbal Pauchard https://orcid.org/0000-0003-1284-3163
Martin A. Nuñez https://orcid.org/0000-0003-0324-5479

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SUPPORTING INFORMATION

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

Supporting Information S1. Description of the estimation process of demographic and dispersal parameters for our Range Shifter model through ABC, as well as the model sensitivity analyses.

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