RESEARCH ARTICLE

Integrating mechanical treatment and biological control to improve field treatment efficiency on invasions

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Projecting invasion treatment outcomes and determining controlling efficiency under various management strategies have important implications in field management. Different from herbicide usage that may cause environmental pollution and nontarget effects on native plants, nonchemical (i.e., mechanical) methods, such as mowing and hand weeding, have shown great targeted effectiveness on invasion. However, an interesting and important question that remains unclear is how to reduce the need for repeated applications of mechanical treatments. One possible approach is to integrate mechanical treatments with biological control agents, which can attack and limit invasion spread after being established in the field. We hypothesize that applying mechanical methods to remove invasive plants while establishing biological control agents, then using the established biological control agents to limit future regrowth of invasive plants, will decrease the use of mechanical treatments. To include vegetation dispersal, we developed a spatial modeling framework, using paired logistic equation models of both a resident native plant and an invasive plant, and a biological control agent, to capture the dynamics of native and invasive plants under different treatment scenarios. Specifically, we examined four factors, the initial application location of biological agents, their controlling efficiency, the treatment frequency (how often nonchemical treatment will be applied), and the areal extent of mechanical treatment. We found that explicitly targeted biological control agents showed significantly stronger controlling impacts on invasive plants than did nontargeted agents, whereas a higher treatment frequency could compensate for the drawback of untargeted treatment. Our results also suggested that adding mechanical treatment can further limit invasion spread with the cooperation of established biological control agents, and applying mechanical treatment in a lower frequency, but treating larger areas per time, is a more efficient approach than vice versa. We emphasize that a high biological control efficiency can continuously decrease the requirement of repeated treatment of nonchemical methods and maintain the invasive population at a low level. The model we developed here can be potentially extended and used by field managers on prioritizing controlling efforts to achieve a higher efficiency.

Keywords: Spatial model, Logistic equation, Predator–prey model, Dispersal, Biological control agents, Mechanical treatment, Adaptive control

Introduction

Biological invasion is a global threat that often drives local biodiversity loss and habitat degradation (Mainka and

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Howard, 2010; Simberloff et al., 2013), and we are facing numerous management challenges (Diagne et al., 2021). One possible explanation of success of an invasive plant is the lack of natural enemies of the alien plants in new regions (Keane and Crawley, 2002). The decreased need to put resources into anti-herbivore success contributes to invasive species ability to grow and reproduce at a faster rate than native vegetation and thus outcompete it. The introduction of specialist herbivores, such as classical (inoculative) biological control agents (Van Lenteren, 2012), from the home range of invasive species, has been observed to successfully attack (Clewley et al., 2012) and reduce the dominance of invasive species in case studies (Tipping et al., 2008; Rayamajhi et al., 2010), ultimately facilitating the recovery of native plants (Zhang et al., 2017).

Despite biological control agents having successfully limited invasion spread in numerous studies, a management challenge still occurs since biological control programs could fail or have limited treatment efficiency due to unsuccessful field establishment (Myers, 2000; Paynter, 2005). Furthermore, field applications of biological control are designed to treat/target explicitly locations of invasive populations. However, in some cases, the application of biological control agents is random over the entire region and includes places where invasive populations have not yet spread (Grevstad, 2006). The difference in the long-term effectiveness of biological control agents between different levels of efficiency and initial treatment locations remains largely untested.

As an alternative to biological control programs, herbicide usage may be a less costly alternative than supplementing biological control agents. Nonetheless, it is generally undesirable due to its polluting effect (Carvalho, 2017) and its nontarget effects, including lasting negative effects on native plants (Flory and Lewis, 2009). Alternatively, mechanical methods, for example, mowing and hand weeding, have shown higher targeted effectiveness in field invasion control (Flory and Lewis, 2009) with limitations such as high labor costs and frequently required repeated treatments. However, mechanical removal is often non-affordable or impractical on a large scale, and costs of control generally far exceed the value of invaded land (Zachariades et al., 2011). Therefore, to minimize the repetition of nonchemical treatments and achieve a high controlling efficiency, we propose a new and promising strategy of integrating nonchemical approaches with biological control treatments. We hypothesize that it is more efficient and less costly to use mechanical methods to remove a proportion of occurring invasive populations while establishing biological control agents in the field, then use the established biological control agents to limit future invasion and decrease repetition of mechanical treatments. Although long-term field data on the outcomes of the interaction of biological control and other management efforts, such as handling removal, are scarce, field efforts have been made in some aggressive invasive species. For instance, the combination of biological, herbicidal, and mechanical control efforts has yielded an Everglades Protection Area that is now largely free of melaleuca quinquenervia (Ferriter et al., 2006; Center et al., 2012). However, to what extent the use of mechanical methods will be minimized by incorporating treatments of biological control is unclear.

Another management challenge that needs to be determined is how to prioritize resource allocation among multiple infested regions. For instance, given the same amounts of effort (or dosage) of treatment, that is, total abundance of biological control agents, total treatment times of mechanical management, it is unclear whether managers should treat smaller areas at a higher frequency or larger areas at a lower frequency (Arroyo-Esquivel et al., 2019; Zhang et al., 2020). Such knowledge will help determine the optimal treatment frequency and size covered in treating spatial clusters of individuals formed by the invading population (Ferguson et al., 2001; Keeling et al., 2001; Dye and Gay, 2003).

To improve understanding of the above management challenges, we developed a spatial modeling framework of using paired logistic equations to capture the competition and dynamic change of competing invasive and native species. We added a predator–prey function to describe the effect of abundance caused by the biological control agents. We further simulated mechanical treatment methods by removing all invasive populations in the treated areas to identify cooperative effects of mechanical methods and biological control program. Although a strong dispersal ability has been recognized as a fundamental driver of biological invasion (Bradley et al., 2010), due to dispersal impacts on species range expansions (Hurtt and Pacala, 1995; Levine and Murrell, 2003), previous modeling work has generally lacked consideration of dispersal process (Hastings et al., 2006; Blackwood et al., 2010; Epanchin-Niell and Hastings, 2010; Bonneau et al., 2019). Hence, we built this model on a spatially explicit gridded region, in which there is dispersal of both vegetation species and biological control agents from given initial cells to the neighboring four cells (up, down, left, and right). Considering species dispersal further allowed us to simulate dynamics in a spatial content where multiple regions are connected by dispersal. We used this model to test three hypotheses: (1) Targeted treatment of biological control is more efficient than the random and nontargeted distributed treatment. (2) Applying a specific dose of treatment effort to smaller regions, but at a high frequency, is more efficient than applying the same total dose to larger regions at low frequency. (3) Integrating mechanical treatment with biological control agents will achieve higher controlling efficiency. Further, the established biological control agents can continuously decrease the requirement of repeated treatment of mechanical treatment and maintain the invasive population at a low level.

Methods and materials
Model framework
We applied a paired logistic equation model describing dispersing hypothetical native (N), invasive (I) populations in a virtual environment, consisting of a 100×100 array of spatial cells (Zhang et al., 2015; see conceptual figure in **Figure 1**). We used a predator–prey model (Hastings, 1977) to describe dispersing hypothetical biological control agents (B) as a function of the population dynamics of invasive species (I) in the region. At every time step, there is added growth of native, invasive, and biological control populations in every occupied spatial cell, ($\Delta N(i,j), \Delta I(i,j), \text{and} \Delta B(i,j)$) (Equations 5–7). A proportion (D_N and D_I) of native and invasive populations disperse and spread equally to the four neighboring cells (up, down, left, and right) at every time step (Equations 1 and 2). According to Marchetto et al. (2014), we assume that biological control populations follow the spread of invasive populations and move more slowly than the invasive species at a rate of D_B. Specifically, we allowed biological
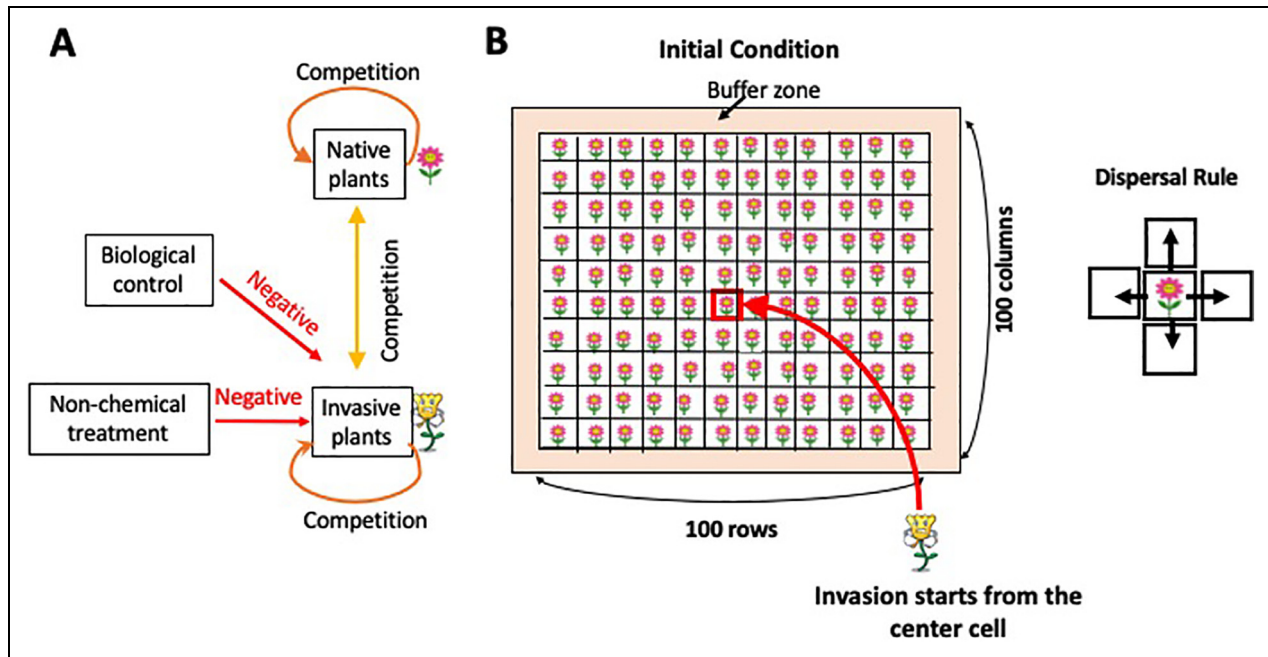
Figure 1. Conceptual description of the model. (A) Schematic figure of the model. (B) The initial condition where native populations occupied all the 100×100 spatial cells and invasive population starts to invade from the center cell. DOI: https://doi.org/10.1525/elementa.2020.00181.f1

control agents to disperse at every 10 time steps (Equations 3 and 4).

The population change every time step in each cell is given by:

$$N_{i,j}(t+1) = N_{i,j}(t) + \Delta N_{i,j}(t) - D_N \Delta N_{i,j}(t)$$
$$+ \frac{1}{4} D_N \big(\Delta N_{i,j+1}(t) + \Delta N_{i,j-1}(t)$$
$$+ \Delta N_{i+1,j}(t) + \Delta N_{i-1,j}(t) \big) \quad (1)$$

$$I_{i,j}(t+1) = I_{i,j}(t) + \Delta I_{i,j}(t) - D_I \Delta I_{i,j}(t)$$
$$+ \frac{1}{4} D_I \big(\Delta I_{i,j+1}(t) + \Delta I_{i,j-1}(t)$$
$$+ \Delta I_{i+1,j}(t) + \Delta I_{i-1,j}(t) \big) \quad (2)$$

$$B_{i,j}(t+1) = B_{i,j}(t) + \Delta B_{i,j}(t) \quad (3)$$

Every 10 time steps, biological control populations disperse

$$B_{i,j}(t+10) = B_{i,j}(t) + \Delta B_{i,j}(t) - D_B \Delta B_{i,j}(t)$$
$$+ \frac{1}{4} D_B \big(\Delta B_{i,j+1}(t) + \Delta B_{i,j-1}(t)$$
$$+ \Delta B_{i+1,j}(t) + \Delta B_{i-1,j}(t) \big) \quad (4)$$

where

$$\Delta N_{i,j}(t) = r \left(\frac{K_{i,j} - \alpha_{11} N_{i,j}(t) - \alpha_{21} I_{i,j}(t)}{K_{i,j}} \right) N_{i,j}(t) \quad (5)$$

$$\Delta I_{i,j}(t) = R \left(\frac{K_{i,j} - \alpha_{22} I_{i,j}(t) - \alpha_{12} N_{i,j}(t)}{K_{i,j}} \right) I_{i,j}(t)$$
$$- \beta I_{i,j}(t) B_{i,j}(t) - H_{i,j} \quad (6)$$

$$\Delta B_{i,j}(t) = \gamma I_{i,j}(t) B_{i,j}(t) - \theta B_{i,j}(t) \quad (7)$$

where i and j are the row and column numbers of the cell; D_N, D_I, and D_B are respectively the dispersal rate of native, invasive, and biological control population; r and R are respectively the intrinsic growth rate of native and invasive population; $K_{i,j}$ is the carrying capacity of cell(i,j) for both native and invasive species; α_{11} and α_{22} are, respectively, the intraspecific competition coefficients of native and invasive populations; α_{21} is the competition coefficient of invasive on native and α_{12} is the competition coefficient of native on invasive; β is the mortality rate of invasive population; $H_{i,j}$ refer to handing removal treatment; γ is the handling and search efficiency of biological control; θ is the mortality rate of biological control.

The Lotka–Volterra model adopted here is widely used for interspecific competition and is reasonable for tree species competing for space and light. We have not assigned spatial units here, but we assume that the scale here corresponds to a landscape or small region, such as a group of counties within a state. If a certain invasive species' dispersal rate (km/year) is known based on field measurement, and since the model assumed it will take a certain population 100 time steps to disperse from one side of the region to another side, the model's spatial scale can then be estimated based on species dispersal rate and dispersal time. For instance, say a species dispersal rate is 1 km/year (Pyšek and Hulme, 2005), and each time step in the model represents 1 year. Then, each cell of the model will represent 1 km in length, and the entire row or column will be $1 \times 100 = 1{,}000$ km in length. Thus, the entire region we simulated here would roughly represent a $1{,}000 \times 1{,}000 = 10^6$ km^2 landscape region.

Initial conditions

We started with a low initial population density of native species where each cell was assumed to have a randomly determined initial population size (N_0) between 0 and 1. Then, an initial invasive population ($I_0 = 2$) started to invade this area from the center cell (row number = 50, column number = 50; see **Figure 1B** for more details). Each cell has the same carrying capacity ($K = 10$). Note that proportions of both an invader and a native can occupy the same cell. No initial biological control agent was applied.

Invasion process

All the scenarios ran for 1,000 time steps. At each time step, a new invasive population ($I_{i,j}(t) = 1$) was added in a randomly selected cell to co-occur with the native population in that cell. This process represents the assumption that invasive species can randomly disperse from outside areas to any new cell on the grid. This can be considered a "worst case" scenario, in which the invasive species is capable of large dispersal events. The spread of native species was assumed to be local.

Dispersal process

A proportion of new populations of native, invasive, and biological control agent populations, ($D_N N(i,j)$, $D_I \Delta I(i,j)$, and $D_B \Delta B(i,j)$), can disperse to neighboring cells and be allocated equally among the four neighboring cells (up, down, left, and right). The dispersal process of plants represents a typical vegetation expansion through the dispersal of seedlings from one cell to surrounding cells. The model is similar to a cellular automata model in which two types of vegetation can be present in any given spatial cell, except that the amounts of vegetation of each type in a given spatial cell are variables described by difference equations. This can be considered agent-based according to some definitions (Bonabeau, 2002). We set the outer two cells on each of the four sides of the plot as a buffer zone, so that they received dispersed populations but did not disperse back. We did not include populations in the buffer zone when we calculated total population abundance.

Biological control

Biological control was simulated as affecting only invasive populations according to the predator–prey function as described in Equations 6 and 7. We simulated two possible field treatment patterns: (1) Targeted treatment—a constant population of biological control ($B_{i,j}(t) = 0.1$) was added to a cell randomly selected from cells that have invasive populations. (2) Untargeted treatment—the same biological control population was added to a randomly selected cell from all the cells. The treatment frequency and efficiency were determined based on each scenario's design as described below.

Mechanical control

We mimic field site-by-site protocol of mechanical treatment (e.g., mowing and hand weeding) as removing the entire row of invasive populations once invasion has been detected in one cell of the row (Güsewell et al., 2000;

Hartman and McCarthy, 2004). Correspondingly, every time when the mechanical control was applied, the model first randomly selected a certain number of non-duplicate cells that have invasive populations. The number of selected cells was determined according to scenarios' design as described below. For instance, if 10 rows of invasive populations are to be removed at every time step, then the model will randomly select 10 non-duplicate cells. All the invasive populations within these selected rows will be removed.

Parameter estimation

The system characteristics represented by parameter values in the model were estimated based on previous findings of general observations between invasive and native species. For instance, invasive species generally are better competitors than natives (Vila and Weiner, 2004; $\sigma_{21} > \sigma_{12}$), and invasives have overall stronger dispersal ability than natives (Nunez-Mir et al., 2019; $D_N < D_I$; see parameter values listed in **Table 1**). In addition, invasive plant populations often have higher growth rate than native populations (Nunez-Mir et al., 2019), but we used the same growth rate for both species because the main focus of this study was to look at the role of competition coefficient and controlling treatments.

Management scenario 1: Comparison of different distribution locations and treatment frequencies with specialist biological control agents

We performed factorial combinations of simulations of biological control treatment with two distribution locations (targeted distribution and untargeted distributions as described above) and two levels of frequency (low frequency—biological control was added every 100 time steps, and high frequency—biological control was added every 25 time steps). We used an intermediate efficiency level of biological control for this scenario ($\gamma = .01$).

Management scenario 2: Comparison of different distribution locations of specialist biological control agents and mechanical treatment frequencies

We performed factorial combinations of simulations with two distribution locations of biological control agent (targeted distribution and untargeted distributions as described above) and two levels of mechanical treatment frequency (low frequency—treat 10 randomly selected rows every 100 time steps, and high frequency—treat one randomly selected row every 10 time steps). We expect, given specific amounts of effort (or dosage) of available controlling treatment, managers can treat smaller areas if they treat in a high frequency, vice versa. Hence, we used the same number of total rows being treated between the low- and high-frequency treatments to represent the same total dose of treatment efforts. We used an intermediate efficiency level of biological control for this scenario ($\gamma = .01$).

Table 1. Parameter values used in the model. DOI: https://doi.org/10.1525/elementa.2020.00181.t1

Description	Native		Invasive	
	Symbol	Default Value	Symbol	Default Value
Intrinsic growth rate	r	0.2	R	0.2
Intraspecific competition coefficient	σ_{11}	1	σ_{22}	1
Interspecific competition coefficient	σ_{12}	1	σ_{21}	2
Mortality rate due to biological control	NULL	NULL	β	0.001
Dispersal rate	D_N	0.1	D_I	0.2
Initial population	N_0	Rand (0–1)	I_0	2
	Biological control agent			
	Symbol		Default Value	
Handling and search efficiency	γ		[0.002, 0.01]	
Mortality rate	θ		0.05	
Dispersal rate	D_B		0.1	
Initial population	B_0		0.1	
	Plot			
	Symbol		Default Value	
Carrying capacity	K		10 for all cells	
Row	i		100	
Column	j		100	

Management scenario 3: Comparison of combined effects of different efficiencies of targeted biological control agents and frequencies of mechanical treatment

We performed factorial combinations of simulations with two levels of efficiency of targeted biological control agents (low, $\gamma = .002$, and intermediate, $\gamma = .01$) and six treatment frequencies of handling removal, as described in **Figure 2A**. For instance, Treatment 1 had the highest frequency by removing invasive populations every 50 time steps, while Treatment 6 had the lowest frequency by treating only every 500 time steps. The total treatment times of the six conditions were as follows: 20, 15, 12, 8, 5, and 2, respectively. Each time when the mechanical treatment was applied, 10 randomly selected rows of invasive populations were removed. The goal here is to identify to what extent biological control can decrease the frequency or the total number of treated rows of mechanical treatments but still maintain invasive populations at a relatively low level.

Management scenario 4: Adaptive mechanical treatment with a combination of different efficiencies of targeted biological control agents

In contrast to Scenario 3, where the mechanical treatment frequency was previously determined and stayed constant through the entire process, here we switched to another strategy—adaptive management. We hypothesized that an efficient invasion control relies on both advisable selections of control methods and adaptive application of control practices. Hence, mechanical treatment was automatically added to simulations when the fraction of invasive population (fraction$_{\text{In}}$) $\left(\frac{\text{su}(I)}{\text{sum}(N)+\text{sum}(I)} \right)$ exceeded 0.2. We chose 0.2 because it was the threshold level of invasive occupancy between the weak and intermediate efficiency level of biological control in **Figure 2B** and **C**. We simulated two levels of biological control efficiency (low ($\gamma = .002$) and intermediate ($\gamma = .01$)) and two numbers of rows being removed by each mechanical treatment (low—remove one row, and high—remove 10 rows).

All sub-scenarios were run for 1,000 time steps and repeated 50 times to consider several stochastic processes involved in this model, for example, the addition of invasive population to a randomly selected cell, the location of applying biological control or mechanical treatment. We calculated the fraction of invasive population (fraction$_{\text{In}}$) $= \frac{\text{su}(I)}{\text{sum}(N)+\text{sum}(I)}$ to represent the level of landscape occupancy of the invasive species at any given time. We saved the final fraction of invasive (Final_fraction$_{\text{In}}$) in each repetition to perform statistical analysis.

Statistical analysis
Scenario 1
Final proportion of invasive (Final_fraction$_{\text{In}}$) as a function of distribution locations and treatment frequencies of specialist biological control agents was determined.

A generalized linear model (GLM) was used to analyze the effects of distribution location (targeted, untargeted)
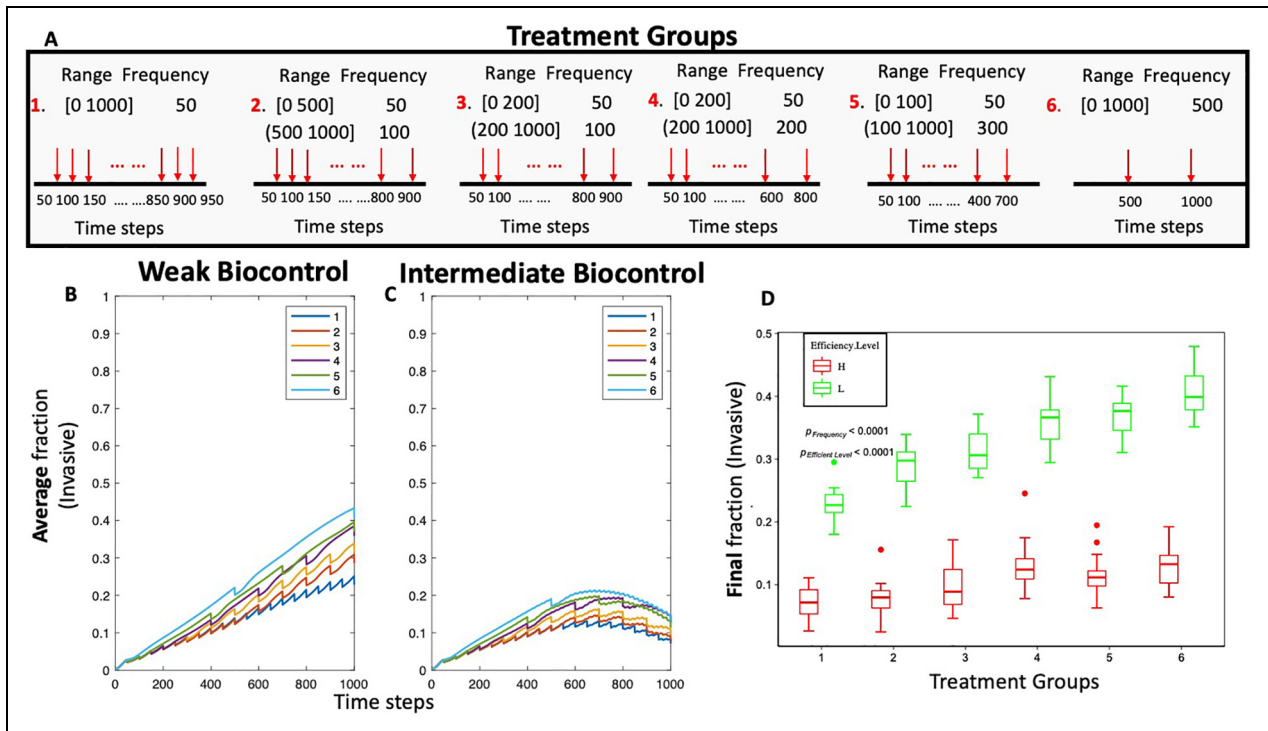
Figure 2. Population dynamics change under interaction of biological control and different frequencies of mechanical treatments. The description of the six treatment frequencies of mechanical treatments (A), the change of average proportion of invasive species over time steps with weak biological control (γ) = .002 (B), with intermediate biological control (γ) = .01 (C), and the final fraction of invasive species across the six treatment groups under weak and intermediate level of biological control (D). DOI: https://doi.org/10.1525/elementa.2020.00181.f2

and treatment frequency (low and high) on final fraction of invasive (Equation 8).

$$\text{Final\_fractionIn}_{i,j} = \beta_{1,i} \times R_i + \beta_{2,j} \times F_j + \beta_{3,i,j} \times R_i \times F_j$$
$$+ \beta_0 + \varepsilon_i, \varepsilon_i \sim N\left(0, \sigma_t^2\right) \dots \dots$$
$$(8)$$

where $\text{Final}_{\text{fractionIn}_{i,j}}$ was the final fraction of invasive at a given condition of distribution location (i) and treatment frequency (j), respectively. $\beta_{1,i}$ was the coefficient of R_i (the ith level of distribution location factor), $\beta_{2,j}$ was the coefficient of F_j (the jth level of fixed treatment frequency factor), $\beta_{3,i,j}$ was the coefficient of interaction of R_i and F_j, β_0 was the intercept, and ϵ_i was the residual in Equation 8. The model selection and assumption examination followed the procedures in (Zuur et al., 2009). The model selection was based on Akaike information criterion (AIC) of models with different variance and covariance (or random) structures. The fixed-effect structure was determined by AIC calculated from maximum likelihood; thus, the interaction of distribution locations and treatment frequencies of specialist biological control agents on $\text{Final}_{\text{fractionIn}_{i,j}}$ was removed. The violation of normality in Equation 8 was visually checked by a Q–Q plot. The violation of homogeneity and independence of Equation 8 were examined by checking residual plots along the fitted values and levels of distribution location and treatment frequency. The above statistical analyses were made by the R program (Kuhn et al., 2020) and the "nlme" package (Pinheiro et al., 2012).

Scenarios 2 and 3 followed the same statistical analysis as described in Scenario 1 with corresponding change in variables. In Scenario 2, GLM was used to analyze the effects of distribution location of biological control (targeted, untargeted) and treatment frequency of mechanical treatment (low and high) on final fraction of invasive. In Scenario 3, GLM was used to analyze the effects of handling efficiency of targeted biological control agents (low and intermediate) and treatment frequency of mechanical treatment (six conditions) on the final fraction of invasive plants.

Results
Scenario 1
We compared the effectiveness of controlling invasive populations using targeted or nontargeted biological control agents in two treatment frequencies. For each of the five sub-scenarios, we randomly selected one simulation run from the 50 repetitions and plotted the final population distribution patterns of native, invasive, and biological control agent in **Figure 3A–E**. First, when no biological control was added, we found a continuous increase in the fraction of invasive species over time (**Figure 3A**), which suggested that invasive species could prevail native species without controlling treatment. The temporal change of average fraction of invasive population of each treatment with biological control is shown in **Figure 3F**. Overall, we found that for both cases of targeted and nontargeted treatments, high-frequency treatments (blue and red lines in **Figure 3F**) resulted in a much lower
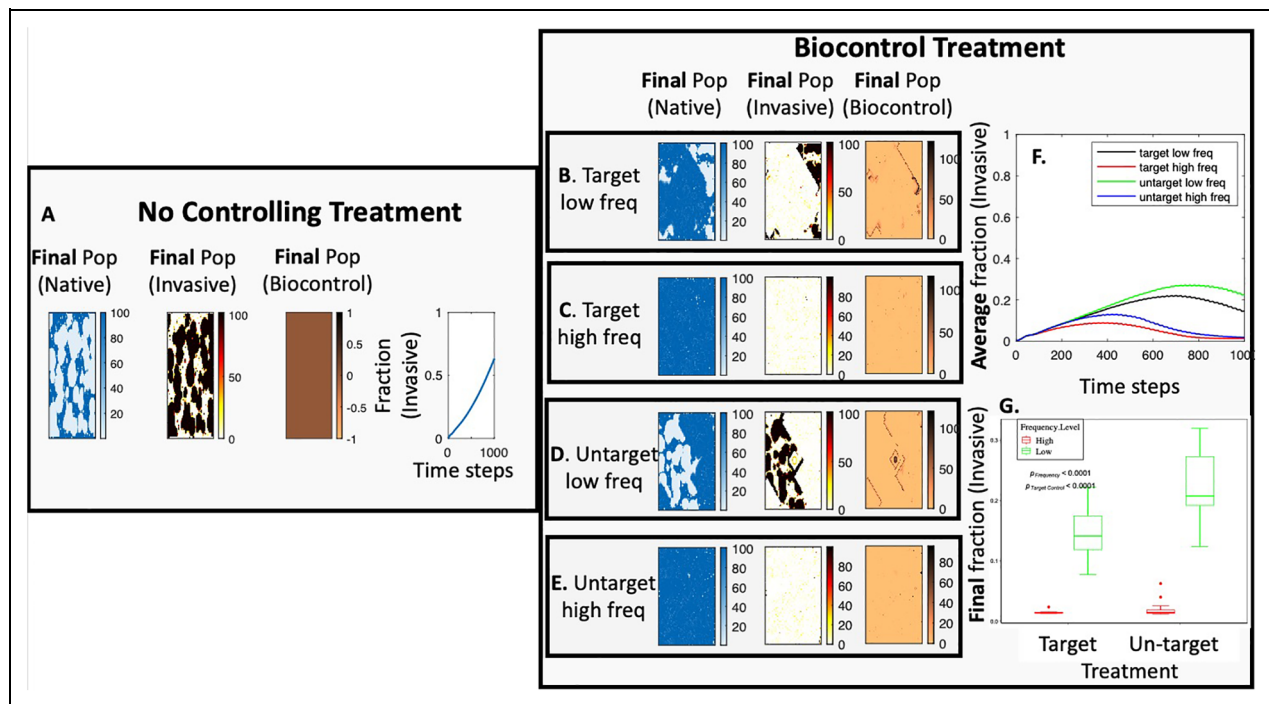
Figure 3. Population dynamics change under different scenarios of biological control. The final population distribution pattern of native, invasive, and biological control agent with no biological control (A), with targeted and low frequency treatment of biological control (B), with targeted and high frequency treatment of biological control (C), with nontargeted and low frequency treatment of biological control (D), with nontargeted and high-frequency treatment of biological control (E), the change of average fraction of invasive species over time steps under the four sub-scenarios (F), and the final fraction of invasive species across the four treatments (G). Biological control efficiency level (γ) = .01. DOI: https://doi.org/10.1525/elementa.2020.00181.f3

fraction of the invasive population than low frequency treatments (green and black lines in **Figure 3F**). Additionally, with the same treatment frequency, the targeted distribution of biological control (black and red lines in **Figure 3F**) showed generally a better controlling outcome than the nontargeted groups (green and blue lines in **Figure 3F**), and the difference was especially greater in the early stage (approximately 400 time steps) than the later stage (after 800 time steps; **Figure 3F**). Overall, both distribution location and treatment frequency showed significant effects on the final fraction of invasive population (p_distribution < 0.0001, p_frequency < 0.0001, sample size = 50; **Figure 3G**).

Scenario 2
Based on Scenario 1, we found that low frequency treatments of biological control had limited controlling effects on invasive species (fraction of invasive species > 0.2). Thus, we asked whether adding a certain level of mechanical treatment (e.g., handing removal) could decrease invasive populations to a lower level. Similar to Scenario 1, we randomly selected one simulation run from the 50 repeated times and plotted the final population distribution pattern of native, invasive, and biological control agents in **Figure 4A–D**. Across all the four sub-scenarios, we observed a consistent pattern that the average proportion of the invasive population increased first then decreased around time step of 600 (**Figure 3E**), which was possibly a result of the successful

establishment of biological control agents. Importantly, compared to Scenario 1, under the same biological control treatment, adding mechanical removal always decreased fraction of invasive population to a lower level (<0.2). Interestingly, our results indicated that applying mechanical treatment at a lower frequency but treating larger areas per time (green boxes in **Figure 4F**) is a more efficient approach than treatment at lower frequency of larger areas (red boxes in **Figure 4F**). Overall, we found both distribution location of biological control agents and treatment frequency of mechanical treatment showed significant effects on the final fraction of invasive population (p_distribution < 0.0001, p_frequency = 0.0012, sample size = 50; **Figure 3F**).

Scenario 3
Given that a high frequency addition of mechanical treatment further limited invasion spread in Scenario 2, it was felt that it is more useful to identify whether biological control can not only maintain invasive populations at a low level but also decrease repetition of mechanical treatment. Here, we compared a gradient of frequency of mechanical treatment from a high frequency (every 50 time steps in Treatment 1) to a low frequency (every 500 time steps in Treatment 6; **Figure 2A**) under both low and intermediate levels of biological control efficiency. With a low efficient biological control agent, we noticed a continuous increase of invasive populations across all the six frequency groups (**Figure 2B**), indicating that an
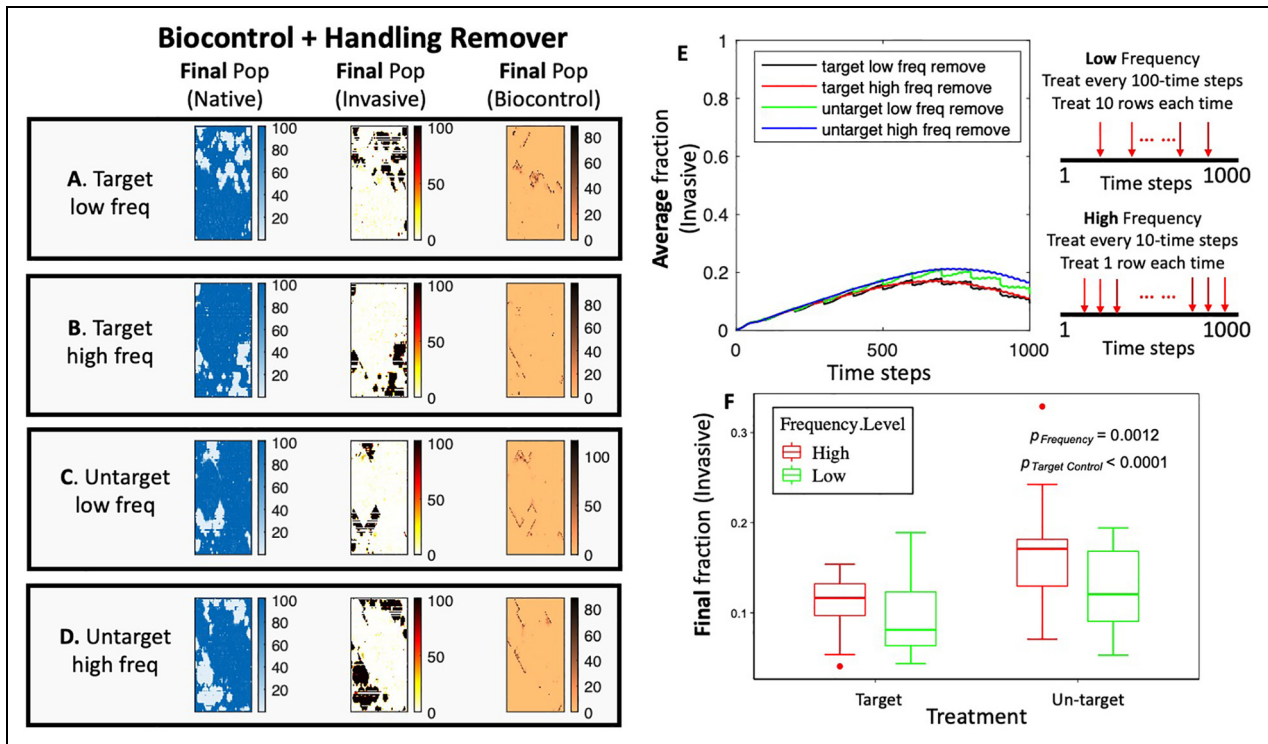
Figure 4. Population dynamics change under interaction of biological control and mechanical treatments. The final population distribution pattern of native, invasive, and biological control agent with targeted biological control and low frequency mechanical treatments (A), targeted biological control and high frequency mechanical treatments (B), with nontargeted biological control and low frequency mechanical treatments (C), with nontargeted biological control and high frequency mechanical treatments (D), the change of average fraction of invasive species over time steps under the four sub-scenarios (E), and the final fraction of invasive species across the four treatments (F). Biological control efficiency level (γ) = .01. DOI: https://doi.org/10.1525/elementa.2020.00181.f4

even higher frequency of mechanical treatment may be needed when biological control was not strong enough to hold off the invasion. On the contrary, with an intermediate level of biological control efficiency, the fractions of invasive population all increased at first and then decreased (<0.2) across all the six frequency groups, suggesting that a stronger biological control treatment could compensate for the less repetition of mechanical treatment, at least to some degree (**Figure 2C**). Compared to Scenario 2 where a same efficiency level of biological control was simulated, we noticed that a lower frequency of mechanical treatment (i.e., 8, 5, and 2 times) led to similar controlling outcomes as higher frequencies (>10 times), indicating that less mechanical treatment may actually be needed with the cooperation of established biological control agents. Furthermore, we found a similar controlling pattern across the six treatment frequencies with an intermediate efficiency of biological control (red boxes in **Figure 2D**) to that of the low efficiency group (green boxes in **Figure 2D**), suggesting that a stronger level of biological control agents may reduce mechanical treatment repetition. Overall, both efficiency level of targeted biological control and treatment frequency of mechanical treatment showed significant effects on the final fraction of invasive population (p_efficiency < 0.0001, p_frequency < 0.0001, sample size = 50; **Figure 2D**).

Scenario 4

In this scenario, mechanical treatment (i.e., handling removal) was applied only when the fraction of invasive populations exceeded the level of 0.2. Under each sub-scenario, we plotted total times that mechanical treatments (i.e., handing removal) were added in each simulation repetition (50 times; **Figure 5A**, **C**, **E**, and **G**) and the temporal change of average fraction of invasive species in each repetition (**Figure 5B**, **D**, **F**, and **H**). We noticed a dramatic difference in how many times handling removal was needed across the four sub-scenarios. Compared to a weak level of biological control that needed 265 $\pm$ 35 or 27.4 $\pm$ 3.5 times of mechanical treatment when one or 10 rows were removed each time, respectively (**Figure 5A** and **C**), an intermediate level of biological control dramatically reduced the total number of times of mechanical treatment to 23.2 $\pm$ 20 or 3.7 $\pm$ 3.1 times (**Figure 5E** and **G**). More importantly, regardless of the efficiency level of biological control, removing one row per time was only able to maintain the invasive population level around 0.2 (**Figure 5B** and **F**). Alternatively, removing 10 rows per time not only continuously decreased invasive populations to a lower level but also reduced total times of treatment (**Figure 5D** and **H**). Among the four subscenarios, integrating efficient biological control treatments with mechanical removal of 10 rows per time resulted in the best controlling outcomes. Compared to the
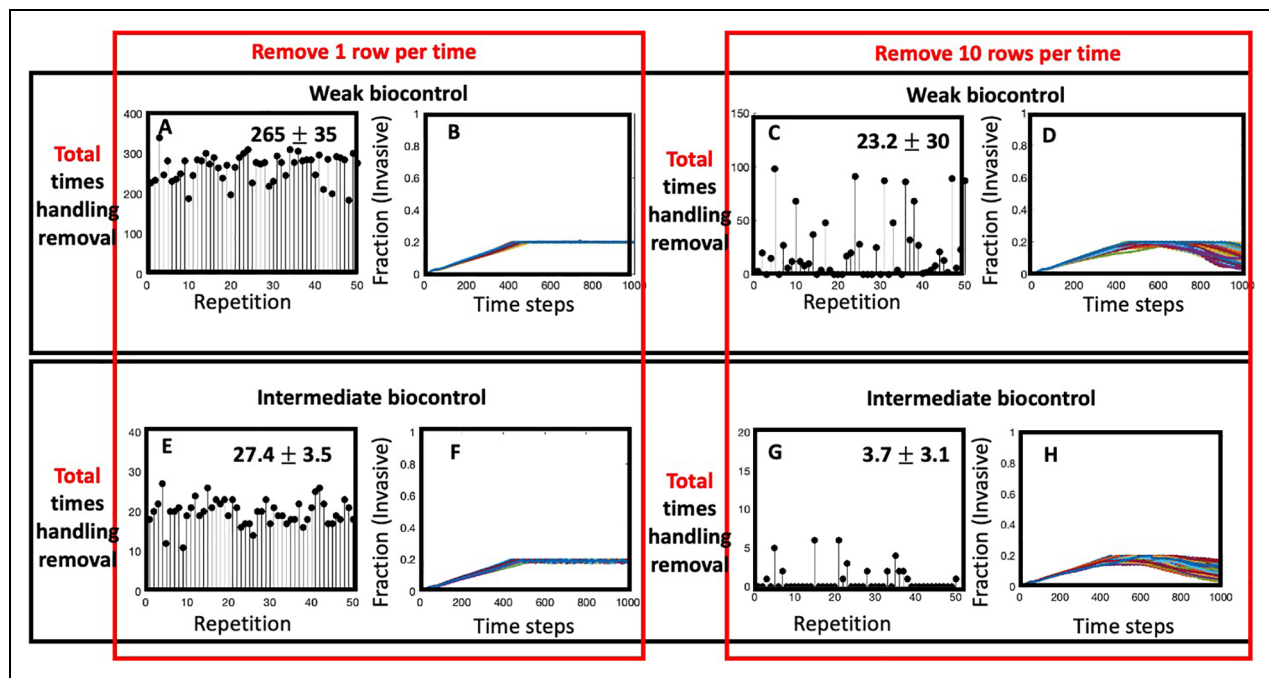
Figure 5. Total times of mechanical treatment under different levels of biological control. Total times that mechanical treatment (i.e., handing removal) were added in each repetition (50 times; A, C, E, and G) and temporal change of average fraction of invasive species in each repetition (50 times; B, D, F, and H) in conditions of weak level of biological control (γ) = .002 with handling removing one row each time (A, B); weak level of biological control (γ) = .002 with handling removing 10 rows each time (C, D); intermediate level of biological control (γ) = .01 with handling removing one row each time (E, F); intermediate level of biological control (γ) = .01 with handling removing ten rows each time (G, H). Note that we used vertical lines to connect data points with corresponding repetition points in A, C, E, and G to give a better vision of the plot. The mean and standard deviation of total time points that mechanical treatment are shown in A, C, E, and G. DOI: https://doi.org/10.1525/elementa.2020.00181.f5

same intermediate level of biological control treatment in Scenario 3 when mechanical treatment was predetermined (**Figure 2C**), adaptive treatment led to a lower level of invasive populations with much lower frequency of mechanical treatment (3.7 $\pm$ 3.1; **Figure 5G**).

Discussion

1. Targeted treatment of biological control is more efficient than the randomly distributed, nontargeted treatment, whereas a higher treatment frequency could compensate for the drawback of untargeted treatment.

Biological control agents have made important contributions to controlling plant invasion (Fravel, 2005; Tipping et al., 2008; Sevillano et al., 2010; Zhang et al., 2018). We found that biological control treatments that targeted explicitly in locations where invasive plants occurred showed significantly stronger effects on reducing invasions than treatments that randomly spread biological control agents in the entire region, especially with low treatment frequency (**Figure 3G**). Although targeted treatments are more desirable, it is often difficult or almost impossible for field managers to locate biological control agents accurately to only those places where invasive species are located (Clewley et al., 2012). The untargeted treatment could result from limited labor resources,

difficult access to specific field locations, and poor detection on invasion spatial distribution. Therefore, it is useful to note that we showed that a highly frequent treatment of untargeted biological control (blue line in **Figure 3F**) led to a similar controlling outcome as the highly frequent targeted one (red line in **Figure 3F**), suggested that a high frequency of treatment may compensate for the drawback of untargeted treatment. This result has important and practical implications in field management; that is, if managers can not accurately allocate biological control agents into specific locations, increasing treatment frequency would be a compensatory strategy.

2. Applying mechanical treatment at a lower frequency with larger treated areas per time is a more efficient approach than applying at higher frequency to smaller areas.

An essential field management dilemma is how to balance treatment frequency and treatment area, assuming that we do not have enough resources to treat all areas at a high frequency. Our results may help to solve this dilemma. For example, when the total areas being treated were the same, our results showed that treating at a lower frequency with larger treated areas per time is a more efficient approach than vice versa. This result advanced previous field studies that focused mainly on treatment

frequency but lacked consideration of balancing treatment frequency with treatment area (Emery and Gross, 2005; Tang et al., 2009; Tang et al., 2010; Valentine et al., 2012). This result could guide field control management in multiple aspects. First, compared to treating a larger area, it is more difficult and costly to treat at a higher frequency due to traveling and transportation cost. Furthermore, it is essential to note that mechanical treatment was applied to randomly selected rows where invasive populations were located. In other words, the desirable treatment efficiency we showed in our simulations does not require applying mechanical treatment in specific areas, which can dramatically relieve field management pressure of prioritizing certain places. As long as managers could treat sites where invasive species are located, following the field site-by-site protocol of mechanical treatment (Güsewell et al., 2000; Hartman and McCarthy, 2004), treating larger areas per time, together with biological control agents, would lead to successful controlling outcomes.

3. An efficient biological control treatment could continuously reduce the repetition of mechanical treatment and still maintain invasive populations at a low level.

An integrative or adaptive management strategy is a new perspective that has recently received more attention in invasion control but still in the initial phrase, so that field data are lacking. The goal is to minimize the use of mechanical treatment by integrating with biological control agents. While long-term and large spatial scale field data of comparing different integrative controlling approaches are currently unavailable because this integrative concept is new, we envision our simulation results could provide perspectives on this topic to guild field control.

Our results emphasized that the key to successfully minimizing mechanical treatment is the efficiency of biological control agents, as a low efficiency may not achieve this goal. While it is often expected that all biological control programs will work efficiently and successfully when applied to the filed, it is critical to be aware that the efficiency of biological control varies depending on the time and how the biological control is applied. Biological control agents could fail due to different reasons, including unsuccessful establishment (Myers, 2000), technical failure, for example, biological control agents not only attacking invasive species but also attacking the native species (Louda et al., 1997), although modern safety measures regarding introduced control agents make the latter unlikely. Furthermore, well-established biological control agents could still fail to reduce the invader's density, which was demonstrated by the result of field experiment of control knapweed invasion. The experiment featured the introduction of European seed-head flies *Urophora affinis* and *U. quadrifasciata* to British Columbia for the biological control of *Centaurea diffusa* and *C. maculosa*. The herbivores became well established but did not

significantly reduce the weed's density (Harris, 1980; Wade et al., 1980). Hence, our simulation results suggested that aiming to improve field establishment success and controlling efficiency of biological control agents should be the first key step to target in the field.

Once there is an efficient agent, we believe both strategies simulated in Scenarios 3 and 4 could be optimal strategies according to different field conditions. For instance, in Scenario 3, we simulated the condition where treatment timing points were predetermined and did not alter with the dynamic change of invasive populations. That scenario represents conditions when invasion detection is low, and managers are more likely to take a passive controlling strategy. If that is the case, our results suggested that a higher frequency of treatment led to a significantly lower abundance of invasive populations, yet the lowest frequency still limited invasion level below 0.2, especially with the cooperation of established biological control agents. Scenario 4 represents cases when invasion detection is high, and managers tend to be more active and flexible in applying field treatment, possibly because mechanical treatments are practically or financially unfeasible. Our results showed a very promising likelihood of minimizing the repetition of mechanical treatment by increasing detection ability and biological control efficiency.

4. Model extensions

The model framework we developed here could be broadly extended to investigate management outcome in more complex conditions. For instance, we looked at one possible field control pattern as eliminating populations across the selected row, but other controlling patterns could be simulated in our model. For instance, it could be tested how different our results will hold if a different pattern was used, such as removing a fraction of invasive populations in 5 × 5 cells in which the selected cell was in the center. Second, we designed a homogeneous 100 × 100 array of spatial cells with the same level of carrying capacity in all the cells; future work would vary the carrying capacity to determine the role of environmental heterogeneity in altering our results. Another interesting future direction is to explore more complex dispersal patterns, such as understanding the effect of greater dispersal distance of invasive species than native species (Nunez-Mir et al., 2019). Additionally, this study focused particularly on the classical biological control approach because it has been used most frequently against introduced pests (Van Lenteren, 2012), yet we envision the model system we developed here can be modified and applied to other approaches, such as the augmentative biological control program that is mass-reared in biofactories for release in large numbers to obtain an immediate control of pests. Last but not least, our simulation suggested the cost–benefit of biological controls in terms of reducing mechanical treatment and extended time intervals for retreatments.

Competing interests
The authors declare that they have no conflict of interest.

Code availability
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Author contributions
Designed the study: ZF, JZ, BZ.
Performed the simulations: ZF, YL, BZ.
Wrote and revised the paper: All authors.

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