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The optimal controlling strategy on a dispersing population in a two-patch system: Experimental and theoretical perspectives

Bo Zhang [a,b,*], Lu Zhai [a], Jason Bintz [c], Suzanne M. Lenhart [d], Wencel Valega-Mackenzie [d], J. David Van Dyken [e,*]

[a] Department of Natural Resource Ecology and Management, Oklahoma State University, United States
[b] Department of Integrative Biology, Oklahoma State University, United States
[c] Johnson University Tennessee, United States
[d] Department of Mathematics, University of Tennessee, United States
[e] Department of Biology, University of Miami, United States

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ABSTRACT

Invasive species, disease vectors, and pathogens are significant threats to biodiversity, ecosystem function and services, and human health. Understanding the optimal management strategy, which maximizes the effectiveness is crucial. Despite an abundance of theoretical work has conducted on projecting the optimal allocation strategy, almost no empirical work has been performed to validate the theory. We first used a consumer-resource model to simulate a series of allocation fractions of controlling treatment to determine the optimal controlling strategy. Further, we conducted rigorous laboratory experiments using spatially diffusing laboratory populations of yeast to verify our mathematical results. We found consistent results that: (1) When population growth is limited by the local resource, the controlling priority should be given to the areas with higher concentration of resource; (2) When population growth is not limited by the resource concentration, the best strategy is to allocate equal amount of controlling efforts among the regions; (3) With restricted budget, it is more efficient to prioritize the controlling effects to the areas with high population abundance, otherwise, it is better to control equally among the regions. The new theory, which was tested by laboratory experiments, will reveal new opportunities for future field interventions, thereby informing subsequent biological decision-making.

1. Introduction

Invasive species, disease vectors, and pathogens are significant threats to biodiversity, ecosystem function and services, and human health (Crowl et al., 2008). The increased connectivity of the global human population has further amplified the influence of biological invasions and disease outbreaks (Dukes and Mooney, 1999; Sakai et al., 2001; Smith et al., 2007). As the available budget/resource is becoming more limited, understanding the optimal management strategy maximizes the effectiveness with the limited amount of budget/resource, is exceptionally urgent (Chades et al., 2011). However, identifying and quantifying the optimal management strategy is challenging and poorly explored due to the difficulty of prioritizing the available resource among infected regions (McDonald-Madden et al., 2010; Nichols and Williams, 2006; Olson, 2006).

Take infectious diseases as an example. It usually occurs simultaneously in different but interconnected regions (Dye and Gay, 2003; Ferguson et al., 2001; Keeling et al., 2001). In this case, when epidemics allocate the available resources to treat infected individuals, seeking to control in more than one region poses a dilemma of how best to deploy limited resources among different regions. Should preference be given to treating infected individuals in regions with high or low levels of infection, or to equalizing levels of infection in different regions as much as possible (Lipsitch et al., 2000)? Take invasive species as another example. Eliminating or at least controlling invasive species is paramount (Dantonio and Vitousek, 1992; Vitousek, 1990; Wilcove et al., 1998) since invading species cause tremendous economic losses (≈ $120 billion per year solely in the United States) (Pimentel et al., 2005). A similar dilemma occurs according to whether the controlling effort should focus on decreasing invasive plants in the central core area where the plants are more abundant and denser, or in the outlying

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* Corresponding authors at: Department of Integrative Biology, Oklahoma State University, 501 Life Sciences West, Stillwater, Oklahoma 74075 (B. Zhang).

E-mail addresses: bozhangophelia@gmail.com (B. Zhang), vandyken@bio.miami.edu (J. David Van Dyken).

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regions where smaller colonies are starting to occur at low levels (Blackwood et al., 2010; Hulme, 2003).

A large body of mathematical theory has worked on projecting the optimal control strategies regarding a large class of invasion problems using different models (Blackwood et al., 2010; Hastings, 2014; Hastings et al., 2006; Moody and Mack, 1988), such as multiscale hierarchical Bayesian forecasts model (Ibáñez et al., 2009), dynamic spatial modeling (Hastings, 2014; Melbourne et al., 2007), and spatially explicit, individual-based simulation (SEIBS) models (Higgins and Richardson, 1999). Whereas, theoretical findings suggested different controlling strategies. For instance, a density-structured model suggested that prioritizing the removal of low-density subpopulations of invasive species is more efficient than removing high-density subpopulations (Taylor and Hastings, 2004). Alternatively, a species distribution model predicted that focusing on the sites where species are most likely to occur and exerting a moderate amount of effort at these sites is more efficient (Giljohann et al., 2011). Hence, we still do not have adequate knowledge to generalize the optimal strategy due to very limited empirical work that has been performed to validate the existing theoretical conclusions (Bonneau et al., 2019). Another constraint of the existing mathematical theory is the general lack of explicit consideration of the time scales of feedback between the organisms and their resource and the role of dispersal (Wilkinson, 2006).

The goal of this study is to overcome these limitations by developing robust mathematical modeling to identify how to efficiently minimize the total population abundance of target species across space with a given amount of controlling treatment in various controlling scenarios, and further validate our theoretical results by rigorous laboratory experiments. Specifically, we aim to investigate how to optimally allocate the total controlling treatment between the two patches (optimal allocation fraction) and how the optimal allocation fraction varies along a gradient of allocation fraction of growth resource between the two patches. We first used a mechanistic, bottom-up approach with explicit resources (consumer-resource model) to model dispersing population growth in a two-patch system (MacArthur, 1972; Tilman, 1982), where the two patches were connected by population dispersal. We adopted this model framework because it accounts for the resource dynamics as an additional variable (MacArthur, 1972; Tilman, 1982), which is more suitable for describing the effects of environmental heterogeneity and dispersal on population dynamics (He et al., 2019; Ruiz-Herrera and Torres, 2018; Van Dyken and Zhang, 2019; Wang and DeAngelis, 2019; Zhang et al., 2017, 2020a,b). We then conducted rigorous laboratory experiments using high throughput experimental methods in spatially dispersing laboratory populations of the heterotrophic budding yeast, *Saccharomyces cerevesiae*, to verify the mathematical results. This study aimed to answer four questions, mathematically and experimentally: 1. What is the optimal allocation fraction of controlling treatment when population growth is limited by growth resource? 2. Does the optimal allocation fraction hold consistently when population growth is not limited by resource? 3. How does the optimal allocation fraction vary between restricted and abundant controlling treatment? 4. What is the role of dispersal on altering the optimal allocation fraction in the above three scenarios?

2. Materials and methods

2.1. Mathematical simulations

A two-patch consumer-resource model was used to simulate population abundance (P) under different combinations of allocation fractions of resource (X) and controlling treatment (Y) between the two patches. We assumed that, within the range where the population growth is limited by resource, a patch can grow a larger population abundance when contains higher resource but lower controlling treatment (Zhang et al., 2017, 2020a). The dependence of population growth rate and reproduction were calculated according to the allocation fractions of resource (X) and controlling treatment (Y) in each patch and the function was calculated by previous experimental measurements (Zhang et al., 2017, 2020a) (more details below). Only resource was exploitable by populations while the controlling treatment was not exploitable.

Three combinations of scenarios were simulated: i) Low and high levels of total resource (to represent tryptophan in the experiment below); Note that population growth was only limited by resource at the low level. ii) Low and high levels of total controlling treatment (to represent cycloheximide in the experiment below); iii) Low and high dispersal rates (d) (5% and 20%). In each scenario, a series of allocation fractions between the two patches of both resource (X = 0.1, 0.2, … 0.9) and controlling treatment (Y = 0.1, 0.2, … 0.9) in all combinations was performed. Once a combination is picked, the same combination was used for the entire simulation. The simulated total population abundance of the two patches was calculated at all combinations of allocation fractions of resource (X) and controlling treatment (Y) in each scenario. The optimal allocation strategy at each level of resource allocation fraction (X) was defined as the allocation fraction of controlling treatment (Y) resulting the lowest total population abundance.

The model started with the same initial population ($P_{10}^{1} = P_{20}^{1}$) in both patches. To match the experiment, we let population grow for length T corresponding to one day in the experiment, then a fraction (d) of population in Patch 1 was dispersed to Patch 2, the fraction (1-d) of the population in Patch 1 remains, and the fraction (d) of population in Patch 2 was dispersed back to Patch 1. There are eight total growth period (j), which represented eight days growth in the experiment described below. Hence, for j = 2, 3, …, 8, P_{10}^{j}, the initial population at the beginning of time period j, is given by $P_{10}^{j} = dP_2((j-1)T^-) + (1-d)P_1((j-1)T^-)$ where d is the transfer or dispersal rate, $(j-1)T^-$ represents the time at the end the previous day, and $P_2((j-1)T^-)$ *and* $P_1((j-1)T^-)$ mean the populations at the end of the day before the dispersal. P_{20}^{j} is similar. This just says that the initial population level for a growth period are the final time values from the previous growth period adjusted due to dispersal.

A conceptual figure of the model was shown in Fig. 1, and using the new population levels after dispersal, the corresponding system of differential equations is given below (Eqs. (1–4)) during each growth period,

Patch 1:

$$\frac{dP_1}{dt} = \frac{r_{max1} N_1 P_1}{k_s + N_1} - g{P_1}^2 \tag{1}$$

$$\frac{dN_1}{dt} = -\frac{r_{max1} N_1 P_1}{\gamma_1 (k_s + N_1)} \tag{2}$$

Patch 2:

$$\frac{dP_2}{dt} = \frac{r_{max2} N_2 P_2}{k_s + N_2} - g{P_2}^2 \tag{3}$$

$$\frac{dN_2}{dt} = -\frac{r_{max2} N_2 P_2}{\gamma_2 (k_s + N_2)} \tag{4}$$

Where the population abundance in patch 1 and 2 are represented by P_1 and P_2 while the corresponding resource level are N_1 and N_2.

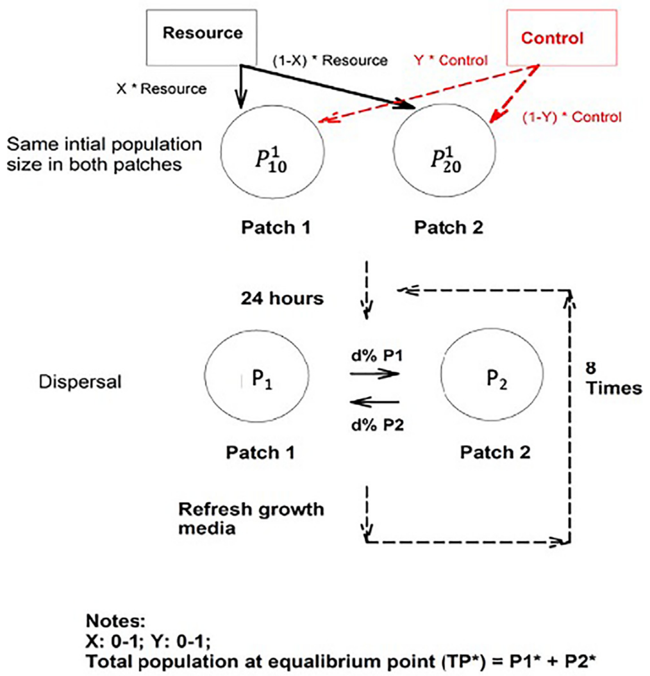

Fig. 1. Schematic figure of the experimental design. All experiments started with the same initial yeast population in Patch 1 and 2 ($P^1_{10} = P^1_{20}$). A fixed total amount of resource (black) was allocated between the two patches at fractions of *X* and *1-X*. Under each resource allocation fraction, a fixed amount of controlling treatment (red) was allocated between the two patches at fractions of *Y* and *1-Y*. The population grew for one day, then a proportion of population in Patch 1 (called dispersal rate, *d*) was dispersed from Patch 1 to Patch 2, then the same proportion of population in Patch 2 was dispersed from Patch 2 to Patch 1. After that, culture media was removed and refilled with fresh media. Both simulation and experiments were run for eight growth periods (days) when the total population reached steady state.

Each choice of total level of resource allocation fraction (X) will determine the resource values of N^j_{10}, N^j_{20}, for the j^{th} growth period, $j = 1, 2, \ldots 8$. The initial values for resource do not, in fact, depend on j: letting N_{total} denote the total amount of resource and X the resource allocation fraction for Patch 1, we have

$$N^j_{10} = XN_{total}, N^j_{20} = (1 - X)N_{total} \text{for all j}.$$

The maximum growth rate for Michaelis-Menten uptake is r_{max} and γ is the yield or consumer production per unit nutrient for each patch. Given the fractions of toxicant control treatment (Y) and the resource allocation, the parameters (r_{max1} r_{max2}, and γ_1. γ_2)) were determined in each patch, and the dependence of these parameters on these fixed fractions were calculated based on previous experimental measurements (Zhang et al., 2017, 2020a). The parameter k_s is the half-saturation constant and g is the density dependent loss rate. We ran the model for eight time periods (j) when the population reached steady state. Total population abundance (P_1 + P_2) was calculated as the sum of population in Patch 1 and Patch 2.

2.2. Experiment

Strain and culture medium: An auxotrophic, haploid strain of the budding yeast, *Saccharomyces cerevisiae*, was used in this experiment to represent an infectious disease or an invasive species. The strain was constructed in the W303 background, with MATa can1-100 hml$\alpha\Delta$::BLE leu9Δ::KANMX6 trp2::NATMX4, provided as a generous gift from M. Muller and A. Murray (Muller et al., 2014). This strain can synthesize all amino acids except tryptophan; therefore tryptophan was used as the limiting growth resource. To mimic a controlling treatment, a yeast toxicant, macrolide eukaryotic antibiotic cycloheximide was used, which decreases yeast population growth and yield through binding eukaryotic ribosomes and inhibiting translation by interfering with translation elongation. The concentration of tryptophan and cycloheximide varied based on the treatment design. The base growth medium consisted of 0.74 g/L of Complete Synthetic Medium minus tryptophan (Sunrise Science) and 20 g/L dextrose for all treatments. All reagents were added to the mixture and then autoclaved to sterilize. In addition, antibiotics tetracycline and ampicillin were added to prevent bacterial contamination. Cultures were propagated asexually.

Establishment and propagation of a two-patch system: All the yeast population was cultured in the round-bottom 96-microwell plates (Costar) and population in each well was one subpopulation. We used two plates as one set and each well at the same location of the two plates together represented one two-patch system. Each patch (well) contained 124 uL of liquid growth medium, as described above, with supplemented with different concentrations of tryptophan (resource) and cycloheximide (controlling treatment) according to design (see below). All patches/wells started with the same initial population. Initial populations were established from a single overnight culture inoculated from freezer stock into 5 mL of YPD (20 g/L yeast extract, 10 g/L peptone, 20 g/L dextrose) and incubated at 30°C with constant agitation in a roller drum shaker. The saturated culture was washed three times with sterile water. 124 uL of this culture was transferred into each well of a 96-well plate, and then diluted by a factor of 2^{10} using a Biomek FXP liquid handling robot.

Experimental treatments: This study was a full factorial design consisting of three factors: total amount of culture resource (tryptophan) (low: 7.34, medium: 22.02 and high: 73.4 mg/L), total amount of controlling treatment (cycloheximide) (low: 700 and high: 1400 nM) and dispersal rate (low: 5% and high: 20%). Based on previous studies, yeast growth was known to only be limited when tryptophan level was at low level (7.34 mg/L) but not limited at intermediate (22.02 mg/L) and high (73.4 mg/L) levels (Zhang et al., 2017)(Zhang et al., 2017). Additionally, we conducted a series of allocation fractions of the resource X (1/5, 2/5, 1/2, 3/5, 4/5) and control treatment Y (1/20, 1/5, 2/7, 2/5, 1/2, 3/5, 2/3, 4/5) between the two patches in all combinations. For instance, the fixed total amount of tryptophan (7.34 mg/L) (black) was allocated between the two patches at fraction of X. If X = 1/5, meaning that 1/5 of the total tryptophan (1.468 mg/L) was allocated to Patch 1 and the remaining 4/5 (5.872 mg/L) was allocated to Patch 2. Similarly, at each tryptophan allocation fraction, the fixed amount of cycloheximide (700 nM) (red) was allocated between the two patches at fraction of Y. 1/20 cycloheximide allocation fraction meant Patch 1 contained 70 nM cycloheximide and Patch 2 had 630 nM cycloheximide. Each treatment had three replicates.

Dispersal protocol: Every 24 h, the 96-well plate was shaken at 1350 rpm on a Titramax 1000 plate shaker to completely disperse the cell pellets. We then measured population density using a microplate photometer (Tecan Infinite M200 Pro) three times, taking the average of these three technical replicates to obtain the optical density at 660 nm (OD_{660}) of each well. After measurement, we used Biomek FXP liquid handling robot to disperse a proportion (d) of media from Patch 1 to Patch 2, then dispersed the same proportion from Patch 2 to Patch 1. To avoid location bias, we alternated the starting patch every day. In addition, we washed cells by centrifuging plates at 2400 rpm for five minutes, removed the supernatant and refilled each cell with fresh medium using a liquid handling robot, to avoid medium transfer. After that, plates were shaken on a plate shaker to completely disperse the cell pellets, then they were incubated unshaken at 30°C for 24 h. Consequently, both nutrients and antibiotics were renewed in periodic pulses every 24 h. Experiments were repeated for eight times, until the populations in both patches reached steady state. Total population at equilibrium was calculated as the sum of final population (OD_{660}) in Patch 1 and in Patch 2.

2.3. Statistical analysis

The optimal allocation fraction of controlling treatment (cycloheximide) (*CyhFrac*) was defined as the one that led to the lowest average total population abundance (red dots in Fig. 3) at each resource (tryptophan) allocation fraction (*TrpFrac*) (1/5, 2/5, 1/2, 3/5, 4/5); see where the arrows are pointing to as an example (Fig. 3). We showed the complete dataset for the cases when $X = 0.2$ and $X = 0.8$ in Fig. 3 and the remaining results were shown in the Appendix, Figs. S2–S12.

To quantify the effects of resource allocation fraction (*TrpFrac*), total resource concentration (*TotalTrp*), total controlling treatment (*TotalCyh*) and dispersal rate on the optimal allocation fraction of controlling treatment (*CyhFrac*), we used a linear regression model (Eq. (5))Eqn 5.

$$CyhFrac_{i,j,k} = TrpFrac + TotalTrp_i + TotalCyh_j + D_k + TrpFrac \cdot TotalTrp_i + TrpFrac \cdot TotalCyh_j + TrpFrac \cdot D_k + \varepsilon_{i,k}, \varepsilon_{i,k}\tilde{N}\left(0, \sigma^2_{i,k}\right) \tag{5}$$

where *CyhFrac* was the optimal allocation fraction of controlling treatment, *TrpFrac* was the corresponding allocation fraction of resource, $TotalTrp_i$ was the i^{th} level of total resource concentration (low: 7.34, medium: 22.02 and high: 73.4 mg/L), $TotalCyh_j$ was the j^{th} level of total controlling treatment concentration (low: 700 and high: 1400 nM), D_k was the k^{th} level of dispersal rate (low: 5% and high: 20%) and $\varepsilon_{i,k}$ was the residuals and assumed heterogeneity between levels of total resource concentration and dispersal. The model selection and assumption examination followed the procedures in (Zuur et al., 2009). In details, the variance and covariance structures of model residuals were determined by comparing Akaike information criterion (AIC) between models with the different structures. The violation of homogeneity and independence were examined by checking residual plots along the fitted values and three independent variables.

3. Results

3.1. Simulation results

With low dispersal rate (5%), when population growth was limited by resource (low total resource level), the optimal allocation fraction of the controlling treatment changed in contingent on the allocation fraction of resource. Consistent with the empirical results described below, the priority should be given to the region contained higher resource as it grew higher population growth (Fig. 2A, B). Differently, when resource level was not limited (high total resource level), we did not find optimal allocation fraction of controlling treatment changed along with resource allocation. Instead, we showed that the optimum allocation fraction was always around 0.5, suggested that it was better to split the control-

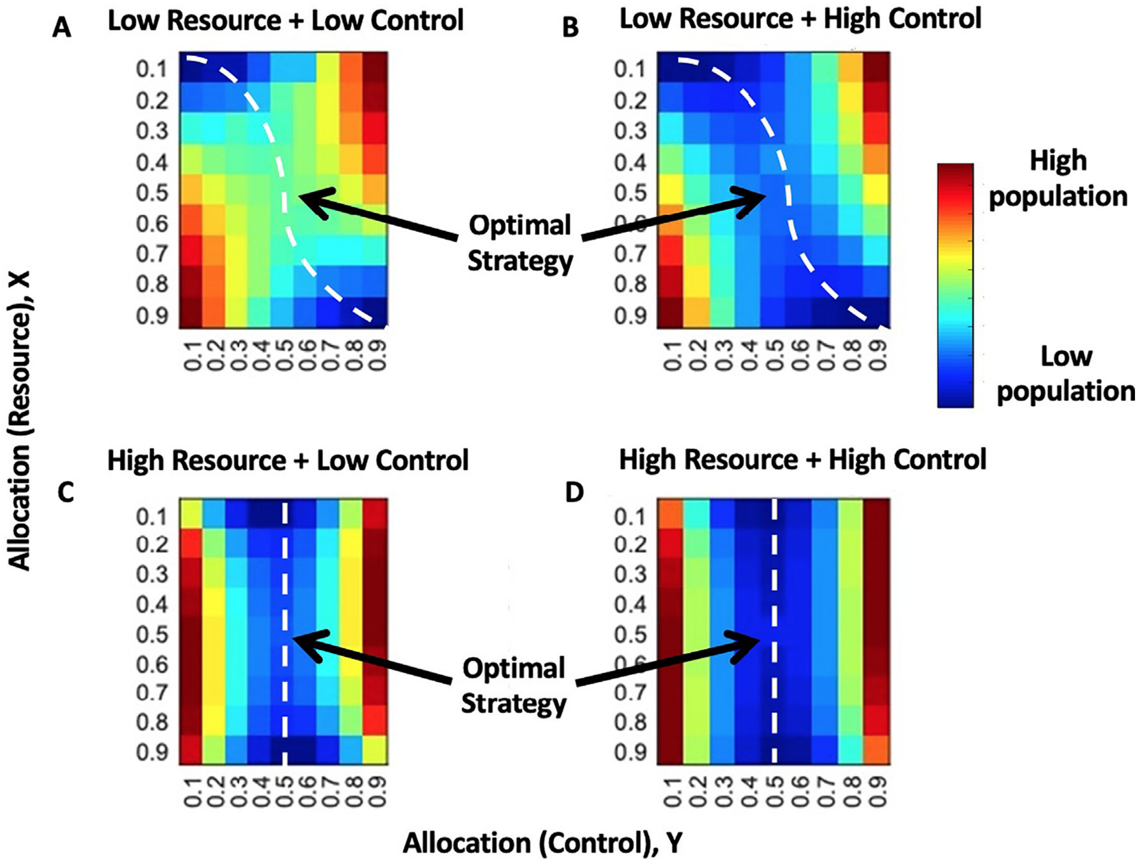

Fig. 2. Simulation of the final total population abundance ($P_1 + P_2$ at the final time) under the combination of a series of allocation fraction of resource (X) and allocation fraction of control (Y) in four scenarios: A: low total resource and low total control; B: low total resource and high total control; C: high total resource and low total control; D: high total resource and high total control. The color of the heat maps quantifies the population abundance. Blue color indicates low total population abundance and red color indicates high total population abundance. The optimal allocation fraction of control, that is, the one that led to the lowest total population abundance, was indicated as the white dashed lines, see where the black arrows point to. Dispersal rate is 5%.

ling treatment evenly between the two patches when population growth was not limited by local resource (Fig. 2C and D). Simulation results with high dispersal rate (20%) are shown in Fig. S1 in the appendix and similar results were found as the scenario with low dispersal rate. We have further performed a broader range of dispersal rate from 5% to 95% at 5% interval. We showed that dispersal rate only changed the optimal allocation fraction of controlling treatment in the scenario with low resource but high controlling treatment (Fig. S2B). When dispersal rate increased, it homogenized population abundance in the two patches and made the two patches more similar. Hence, the optimal allocation fraction tends to be close to 0.5 with higher dispersal rates.

3.2. Experimental results

With low dispersal rate (5%), we found similar associations of total population abundance with allocation fraction of controlling treatment (*Y*) in cases of low resource. The optimal allocation fraction of control to Patch 1 was 0.1 when a fraction of 0.2 resource was allocated to Patch 1 (Fig. 3A and C). Reversely, when a fraction of 0.8 resource was allocated to Patch 1, the optimal allocation fraction of control to Patch 1 increased to 0.6 or 0.7, indicating that when more resource was allocated to Patch 1, it was more efficient to allocate more controlling efforts to Patch 1 correspondingly (Fig. 3B and D). In other words, it was more efficient to minimize total population if more control was given to the patch where there was higher resource to grow larger population size. Consistent to the simulation results, when resource level increased, so that population growth was not further limited, the optimal allocation fraction to Patch 1 was always at 0.5, suggesting that the optimal strategy was to give equal amount of control between the two patches (Fig. 3E–H).

We further plot the optimal allocation fraction of controlling treatment corresponding to all allocation fractions of resource, and we found a significant positive correlation between the two variables with complete data points of all resource and controlling treatment levels ($\beta1$ = 0.72, p = 0.0099) (Fig. 4A). The positive correlation indicated that more control treatment should be prioritized to the area with more resource. Further, when looking at the data only in the low resource or low control conditions, we found a much stronger positive correlations (Fig. 4B and E), whereas, the remaining three cases did not show significant correlations (Fig. 4C, D and F). These results suggested that the positive relationship in Fig. 4A was driven by scenarios when *TotalTrp* = 7.34 mg/L or *TotalCyh* = 700 nM. Meanwhile, the relationship switched to be non-significant at other levels of *TotalTr* and *TotalCyh*, indicating that the optimal allocation strategy was not sensitive to the change of the resource allocation. However, the effects of both dispersal and its interaction with *TrpFrac* on *CyhFrac* were non-significant (p = 0.41 and 0.21, respectively). The complete data were shown in the Appendix Figs. S2–S12.

4. Discussion

Mathematical modeling has made a great effort in guiding on-the-ground management of invasive species, whereas empirical testing was lacking. Our study, combined mathematical modeling and empirical analysis, not only filled in the gap of lack of empirical

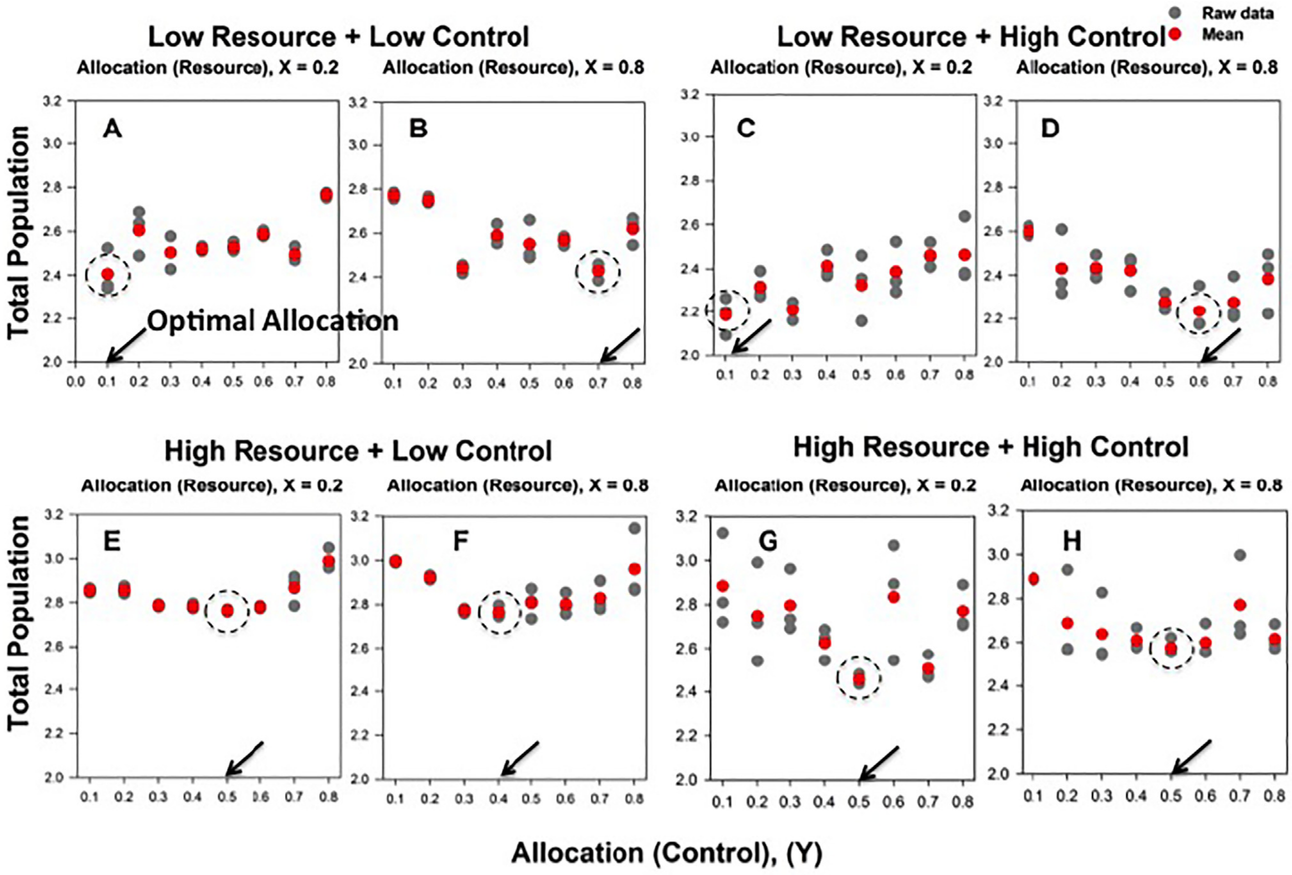

Fig. 3. Empirical results of the final total population abundance along a series of allocation fraction of control (*Y*) when allocation fraction of resource (*X*) were 0.2 and 0.8, in four scenarios: A, B: low total resource and low total control; C, D: low total resource and high total control; E, F: high total resource and low total control; G, H: high total resource and high total control. The optimal allocation fraction, which is the one that resulted in the lowest mean of the total population abundance, is highlighted with the dashed circle and black arrow in each sub-figure. Dispersal rate is 5%. Grey points: raw data and red points: mean of the three replicates.

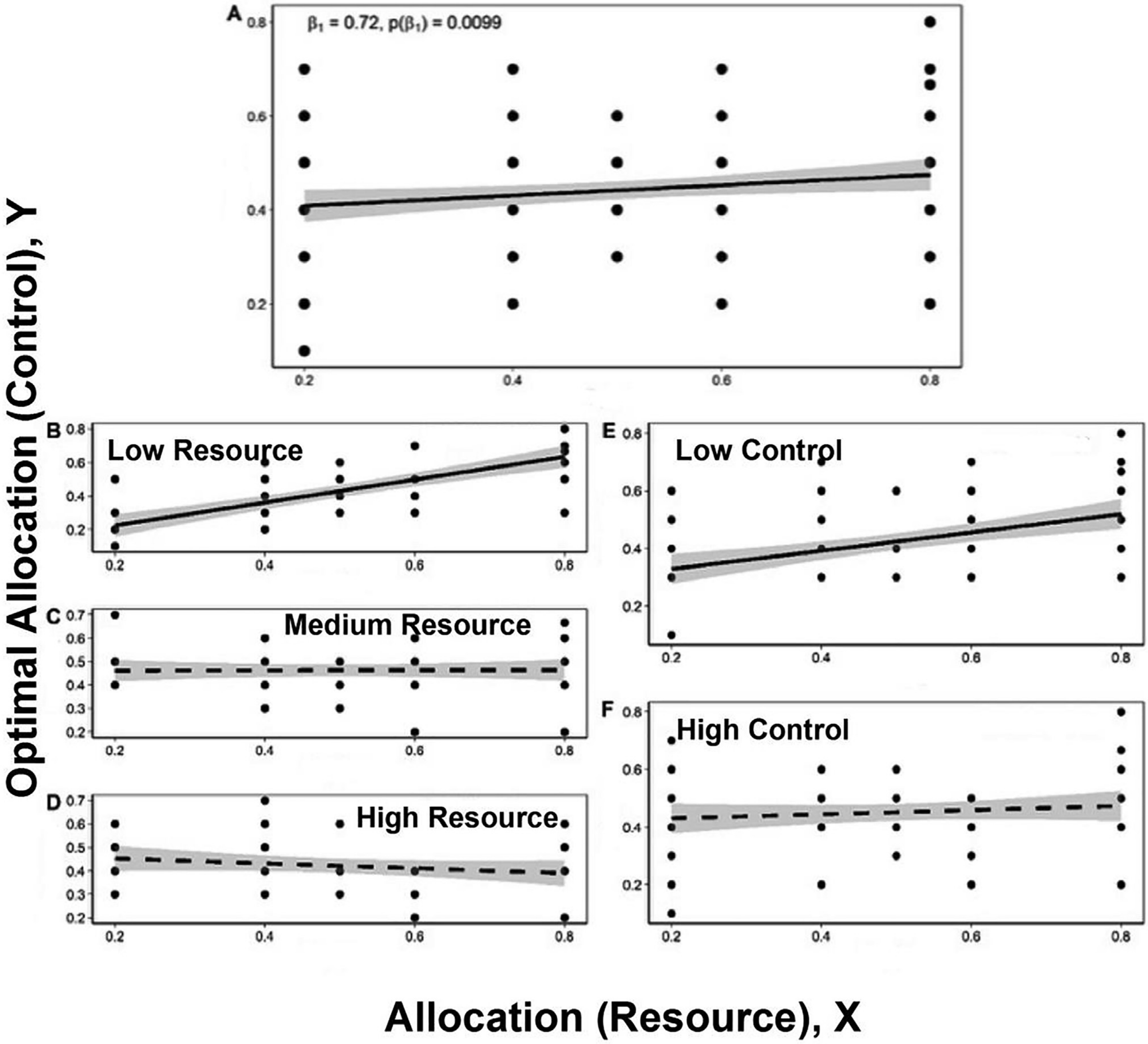

Fig. 4. Correlation of the optimal allocation fraction of control (*Y*) with the corresponding allocation fraction (*X*), A: all data points with all resource and control treatment levels; B: Low total resource; C: medium total resource; D: high total resource; E: Low total control treatment; F: high total control treatment‘. The solid line represents a significant linear correlation and the dashed line represents a non-significant linear correlation.

test but also emphasized a new aspect that the effective management strategy is highly correlated to the distribution of the limiting growth resource. Particularly, when the resource limits population growth, the priority of controlling effort allocation should be given to the areas with higher concentrations of resource. This result provided a new aspect because earlier work mainly focused on determining the optimal strategy of control based on species density/abundance distribution (Menz et al., 1980; Wadsworth et al., 2000), without considering the difficulty of detecting and estimating population density/abundance in the field (Bonneau et al., 2019; MacKenzie et al., 2003). Therefore, when it is impossible to explore as many areas as needed to detect early population establishment, projecting population abundance based on the local resource level is a more accessible solution. In other words, when we understand what the primary limiting resource on population expansion is, we may ultimately decide on an allocation strategy of controlling treatment using the resource distribution as a proxy for the invasive population itself, as long as the population has the potential to arrive at that area by dispersal. For instance, if the invasive species population growth is limited by soil nutrient, e.g., soil nitrogen, the primary controlling effort should focus on the potential infectious area with higher soil nitrogen concentration, because it leads to a lower risk of new propagules (Baker, 2017). Taking disease as another example, climatic factors such as temperature affect disease vector or disease agent survival (Patz et al., 2005). Thus, our results suggest that we should prioritize the controlling treatment to the area with the most suitable temperature and other climatic conditions.

In cases where the resource concentration does not limit population growth, this study showed that the best strategy is to allocate an equal amount of controlling efforts among the regions. There are real situations in which resource limitation is not a limiting factor for population growth. For example, nutrient enrichment, resulting from nitrogen deposition and human activities, releases some invasive species from nitrogen limitation (Brooks, 2003; Fenn et al., 2003)(Brooks, 2003; Fenn et al., 2003). In this case, the most efficient strategy for minimizing the size of pest species is equalizing the treatment level in different regions, which agrees with (Arroyo-Esquivel et al., 2019; Zhang et al., 2020a; Giljohann et al., 2011). One explanation is that when a local resource does not limit population growth, balancing treatment equally among the colonized regions is optimal because population abundance in each region will eventually reach to the same level of carrying capacity. Another reason is that when the resource is not limiting, invaders establish equally quickly, so that keeping strategies constant along space is cost-effective in this case (Holden et al., 2016). It is important to note that this study only investigated the change of total resource level and resource distribution for simple types of spatial heterogeneity, whereas some other factors deserve further empirical and mathematical investigation. For example, a spatial distribution may alter our results because the interaction between dispersal, habitat heterogeneity, and population growth parameters shape carrying capacity in spatial populations (Van Dyken and Zhang, 2019). In addition, we only explored a two-patch system, and so this analysis does not say how multiple patches distribution changes the decisions for using control. Lastly, our study focused on the same low initial population condition in both patches; how different initial population levels might change our results still need to be investigated.

Besides the effect of limiting resources, the availability of controlling treatment/budget also plays a vital role in deciding the optimal allocation strategy. Both our numerical simulation and empirical results found that it is more efficient to prioritize the controlling effects to the areas with high population abundance when the budget is restricted, which is in line with (Meier et al., 2014; Prattley et al., 2007). On the other hand, with sufficient budget, it is better to control equally among the regions. This result is consistent with (Monteiro et al., 2012) that when available, vaccination of the entire population is the most robust strategy. Our results are opposite to (Taylor and Hastings, 2004), which found that at low and medium budgets, it was necessary to remove the low-density plants first to achieve eradication, while, if more money was available, then the optimal strategy was to prioritize high-density areas. It is important to note that (Taylor and Hastings, 2004) used a density-structure model to simulate different age classes of the study objective (*Spartina alterniflora*) and they had also included an Allee effect in their model simulation. However, we did not consider these two factors in our model and experiment because the population our study was applied to has neither age-structure nor Allee effect.

Dispersal rate played a surprisingly ignorable impact on altering the decision of optimal allocation strategy in this study. This finding agreed with (Moore et al., 2011) but disagreed with (Cacho et al., 2010). This is because dispersal did not alter the cost or the effectiveness of management in both the model and the experiment. Besides, this study looked only at a two-patch system, so there was no variation in dispersal rates as there would be if there were more patches and the dispersal probability changed according to the distance among the patches. In that case we might expect a stronger effect of dispersal on the optimal controlling decision. Furthermore, consistent with (Pichancourt et al., 2012), our results indicated that having a precise estimate of population dispersal rate might not be needed to determine the effect of control, mainly because estimating population dispersal rate is very difficult. Finally, we are aware that we have only explored the effect of intermediate dispersal rates (5% and 20%), the consequence of a higher dispersal rate is still a good area of future research.

The experimental and mathematical simulation information, provided consistent results, will help land managers and researchers on making decision of the most effective use of controlling treatment, ultimately, will develop scientific principles to support environmental decision-making. In particular, verifying the theoretical results with empirical data advance previous analytical understanding of the efficacy of various management strategies using a reaction–diffusion model (Bonneau et al., 2016), which will have crucial significance to global conservation.

Authors' contributions

BZ and JDVD designed the study. BZ collected data and performed simulations. LZ carried out statistical analysis. JB and SL performed mathematical analysis. WV made simulation figure. BZ and LZ wrote the first draft of the manuscript. All authors contributed to framing the manuscript, editing and approving the final draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtbi.2021.110835.

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