The role of barrier zones in controlling invasive species: A microcosm experiment

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Abstract

Around the world, invasive species have altered ecosystems, entailing both social and economic consequences. Further, preventing and controlling their spread requires high costs. One common approach to control invasive species is through barrier zones. A barrier zone is a region surrounding an initial invasion where management of the invasive species is conducted, including direct harvesting. Although barrier zones have been examined theoretically and implemented in the field, they have received limited experimental testing, which can provide replication. Here, combined with a mathematical model, we use microcosms of the invasive species, the confused flour beetle (*Tribolium confusum*), to assess the effectiveness of barrier zones and harvesting. We varied both harvesting levels and barrier size and found that barrier zones can be effective tools in both reducing the overall population size and controlling the spatial spread of an invasive species. In our system, increasing barrier size was generally more effective than increasing harvest rate; however, this depends on the relative costs of invasive species damage versus control strategies. Low-effort strategies produced the greatest variability in management outcomes. Together, these results highlight the promise of barrier zones and the importance of considering both desired outcomes and the costs in invasive species management.

Keywords: barrier zone; invasive species management; spatial spread; dispersal; microcosm experiment; stochastic model; Tribolium

Introduction

Invasive species have significant ecological, economic, and social consequences (Kean et al. 2019, Haubrock et al. 2021, Diagne et al. 2021). For example, invasive species in Europe alone cost approximately USD $140.20 billion between 1960 and 2020; these costs spanned multiple sectors and included direct damages, loss of natural resources, and management (Haubrock et al. 2021). However, managing these species is difficult for several reasons. Invasive species often have life histories that make them prolific, such as fast growth rates and the ability to withstand harsh environmental conditions (Sakai et al. 2001, Novoa et al. 2020). Plus, once invasive species are detected in an area, they require additional detection and management (Rout et al. 2014, Lodge et al. 2016). For example, common management strategies (e.g., for prevention, control, education) include direct harvesting, biocontrol, altering habitat, and habitat restoration (Myers et al. 2000, Liebhold et al. 2016, Liebhold and Kean 2019). The costs for these efforts account for upwards of 20% of the total costs of invasive species (Haubrock et al. 2021).

Nonetheless, a promising management strategy for invasive species is barrier zones. Barrier zones have been used (sometimes informally) since the early 1900s, including applications to applications to the Spongy moth and the Brown-tail moth (*Euproctis chrysorrhoea*) (Liebhold et al. 2016, Liebhold and Kean 2019). A barrier zone is “an area at the front of the population distribution where eradication (or suppression) activity is performed in order to prevent or to slow the spread of the population” (Sharov and Liebhold 1998a). Barrier zones are still regularly used in modern efforts to slow or eradicate invasive species. For example, the spread of the Citrus long-horned beetle (*Anoplophora glabripennis*) has been contained in several countries through host removal and chemical pesticides (Liebhold and Kean 2019). Yet, control efforts of other species, such as the Emerald ash borer (*Agrilus planipennis*) have been largely unsuccessful (Liebhold and Kean 2019).

In 1998, Sharov and Liebhold introduced the idea of barrier zones to the invasive species modeling literature (Sharov and Liebhold 1998a,b). They built a theoretical model of the spread of the Spongy moth (*Lymantria dispar*, formerly known as European gypsy moth) in the U.S. to understand optimal control strategies. Their work showed that barrier zones can successfully slow or eradicate invasive species through management efforts such as harvesting, chemical use, physical barriers, and biological control. Despite the extensive modeling and field applications of barrier zones since, several key questions remain. Generally, one of the most difficult obstacles to testing invasive species theory is a lack of replication (Barley and Meeuwig 2016). After an invasive species becomes established, we typically lack information on how many failed invasion attempts took place (Bartell and Nair 2004, Galera et al. 2018). In addition, we typically only have a single population of the invasive species. Further, control efforts may slow or eradicate the species, but this also lacks replication and control groups. Even though the Global Eradication and Response Database (GERDA) has provided an opportunity to study the variability in management responses of the same or similar species (Kean et al. 2019, Liebhold and Kean 2019), this type of meta-analysis still does not provide actual replication. Mathematical models can simulate alternative strategies and stochastic outcomes, but they still do not provide empirical replication.

To overcome some of these obstacles, microcosm experiments can be particularly useful (Benton et al. 2007, Melbourne and Hastings 2008, 2009). For instance, Fryxell et al. (2005) used experimental microcosms to show that a ciliate species could be controlled with different harvesting strategies. In another example, White et al. (2019) used microcosms of the model invasive species, the confused flour beetle (*Tribolium confusum*), to study the variability in potential outcomes of different management strategies. They tested combinations of two control strategies—direct harvesting and slowing dispersal. They show that control strategies of high harvesting and limiting dispersal were the most effective. By replicating each treatment, they were able to show that even moderate levels of the control strategies were highly variable in outcomes between replicates (White et al. 2019), despite being in a highly controlled environment. However, previous work with microcosms has not investigated the effectiveness of more specific forms of management, such as barrier zones.

Here, we use both a mechanistic model and an experimental microcosm to assess the effectiveness of barrier zones in controlling invasive species spread. Specifically, we use microcosms of confused flour beetles (*Tribolium. confusum*). Flour beetles are agricultural pests and have been used as model systems for the development of stage-structured population dynamics, spatial spread, and nonlinear dynamics (Costantino and Desharnais 1991, Henson et al. 1999, Dennis et al. 2001, Melbourne and Hastings 2008, White et al. 2019). With this system, we tested different levels of management, including harvest effort and barrier zone size. Our stochastic model builds on past work (Melbourne and Hastings 2008, White et al. 2019) and includes reproductive and dispersal functions parameterized from prior experiments. We use the model and experiment to test tradeoffs between effort within a barrier zone (i.e., the harvest rate) and the size of the barrier zone. We also examine the sensitivity of management efforts to the selected management objective and underlying population dynamics.

Methods

Simulations

We modified a previously developed simulation framework designed for the model invasive species, the confused flour beetle (Melbourne and Hastings 2008, White et al. 2019). This simulation is a discrete-time model of spatial spread for non-overlapping generations. The spatial landscape is also discrete with a series of distinct patches connected via dispersal, where patch one individuals can move to patch two, patch two individuals can move to patch one or three, and so forth. The model incorporates a Ricker-type function for reproduction and a dispersal kernel for adult movement. We only explicitly model the total number of adult beetles from one generation to the next.

As described in White et al. (2019), we conducted two independent experiments to parameterize this model. Without any dispersal, we placed different initial abundances of beetles in single chambers. We then measured the number of beetles after one generation to parameterize the reproductive function (Table S1). We fit a Ricker-type function that incorporated four sources of stochasticity: (1) demographic stochasticity (births and mortality), (2) environmental stochasticity (variation in the growth rates), (3) demographic heterogeneity (variation in the birth rate between individuals), and (4) stochasticity in offspring sex. The full model description is given in Eqs 2, 3, and 7 in the supplement to Melbourne & Hastings 2009 and Table 1 in the supplement to Melbourne & Hastings 2008.

We parameterized the dispersal kernel (a Poisson dispersal kernel with extra variation given by a Dirichlet-multinomial distribution) with another one-generation experiment where we tracked the distance traveled by adult beetles over different time periods (1, 6, 12, 24, and 48 hours). A summary of all estimated parameter values is given in the supplementary material (Table S1).

Following White et al. (2019), beetles started in patch one and could move during the discrete dispersal windows. We modified past work to include barrier zones and harvesting. Specifically, after reproduction and dispersal, we imposed a management strategy through harvesting, which could vary by amount and location (i.e., the specific patches). A barrier zone could be of different widths; for example, a barrier zone in patch two would be a third of the size (and a third of the harvesting effort) and a barrier zone that spanned patches two through four.

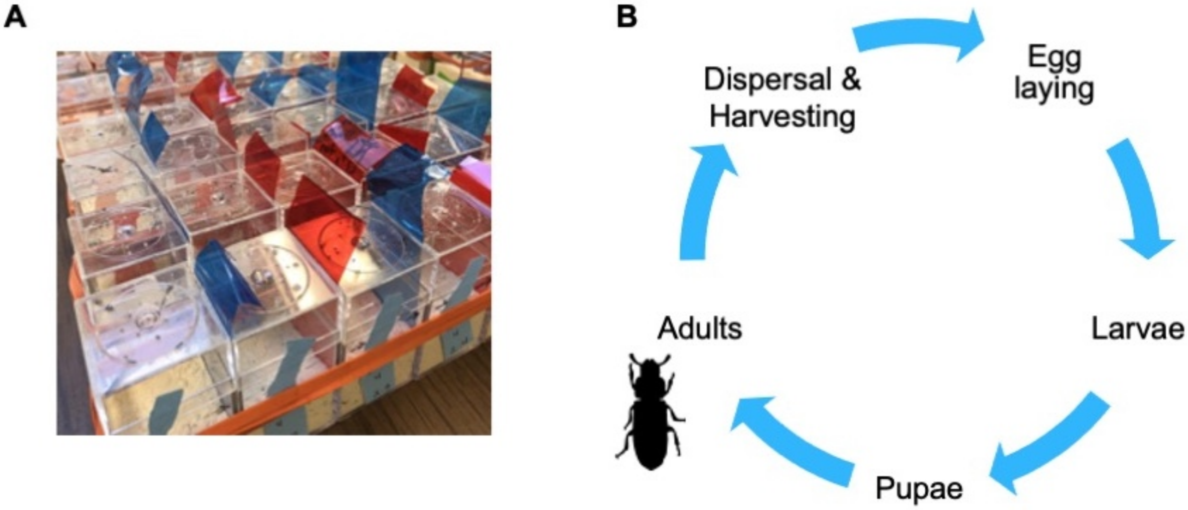

Figure 1: (left) Example experimental landscapes where six patches are connected via small holes, but are kept separate (using the blue and red plastic barriers) during non-dispersal windows. Beetles were always started in patch one with their movement to the right tracked across generations and (right) General experimental and life history dynamics for beetles where each non-overlapping generation lasts six weeks.

Experimental setup

We obtained confused flour beetles (*Tribolium confusum*) from stock populations maintained in 4 × 4 × 6 cm containers with 30 mL of flour and yeast medium. Stock populations were maintained at 31 degrees C and 67% relative humidity. For each replicate, we inoculated patch one with 75 individual adult beetles. These beetles were allowed to lay eggs (with no dispersal allowed) for 24 hours, at which point adult beetles were removed from each patch (Fig. 1). On day 40, adult beetles were allowed to disperse for 48 hours. We controlled dispersal time by removing and replacing the plastic screens between patches. On day 42, we counted adult beetles. Then, we placed a fraction of these adults in fresh medium to start the next generation. The fraction of adults was set by a harvesting function. We chose a fixed-proportion strategy (where a fraction of beetles were harvested) for its simplicity. The different treatments (Table 2) had different harvesting rates in different patches. In cases where a fixed proportion of harvesting resulted in a fraction of a beetle, we rounded up and harvested a whole number of beetles. For example, 30% of 41 beetles = 12.3 beetles; therefore, 13 beetles would be harvested. Adults were then allowed to lay eggs for 24 hours before being removed.

Our design resulted in 12 different landscape treatments (including the controls). The treatments included no harvesting (the control), and 75% harvesting in patch one and 100% harvesting in patch two. We also included treatments of 75% harvesting in patch one, and 100% harvesting in patches two and three, along with 75% harvesting in patch one and 100% harvesting patches two, three, and four. The last of these strategies represented the barrier zone treatment with different-sized widths of barrier zones around patch one. We replicated each treatment 12 times for a total of 96 landscapes (576 total patches). We ran the experiment for four generations (24 weeks).

Analysis

To examine the effectiveness of different management strategies, we used a series of generalized linear models with two general approaches. First, for a response variable based on the beetle count (representing the desired management outcomes), we used a generalized linear model with a Poisson error structure. Second, when we examined whether or not a particular management strategy was successful, as a binary variable, we used a generalized linear model with a binomial error structure. For both types of models, our predictor variables were generation, barrier zone size (i.e., the number of patches and the location where harvesting occurred), and the harvest rate. We used residual plots to verify that model assumptions were met.

Results

Simulations

Our simulated results suggested that harvesting at 100% in a large barrier zone would prevent beetle populations from growing and crossing the barrier zones (Fig. 2). There was little difference between harvesting in patch one or two in terms of the end population size. Similarly, there was little difference between a barrier zone of two or three patches in width (Fig. 2). In general, there was an interaction between harvest rate and the barrier zone size, which makes sense as larger barrier zones overall exerted more control on the population.

Experimental

We found that both increasing harvesting and barrier zone size worked to control invasive species population size and spatial spread (Figs. 2-4). Moderate (h=0.75) harvesting in patch one, where the population was initialized, did very little to control spread compared to the control treatment of no harvesting (Figs. 2-4). However, increasing harvesting rates to 100% within the barrier zones or increasing the barrier zone width

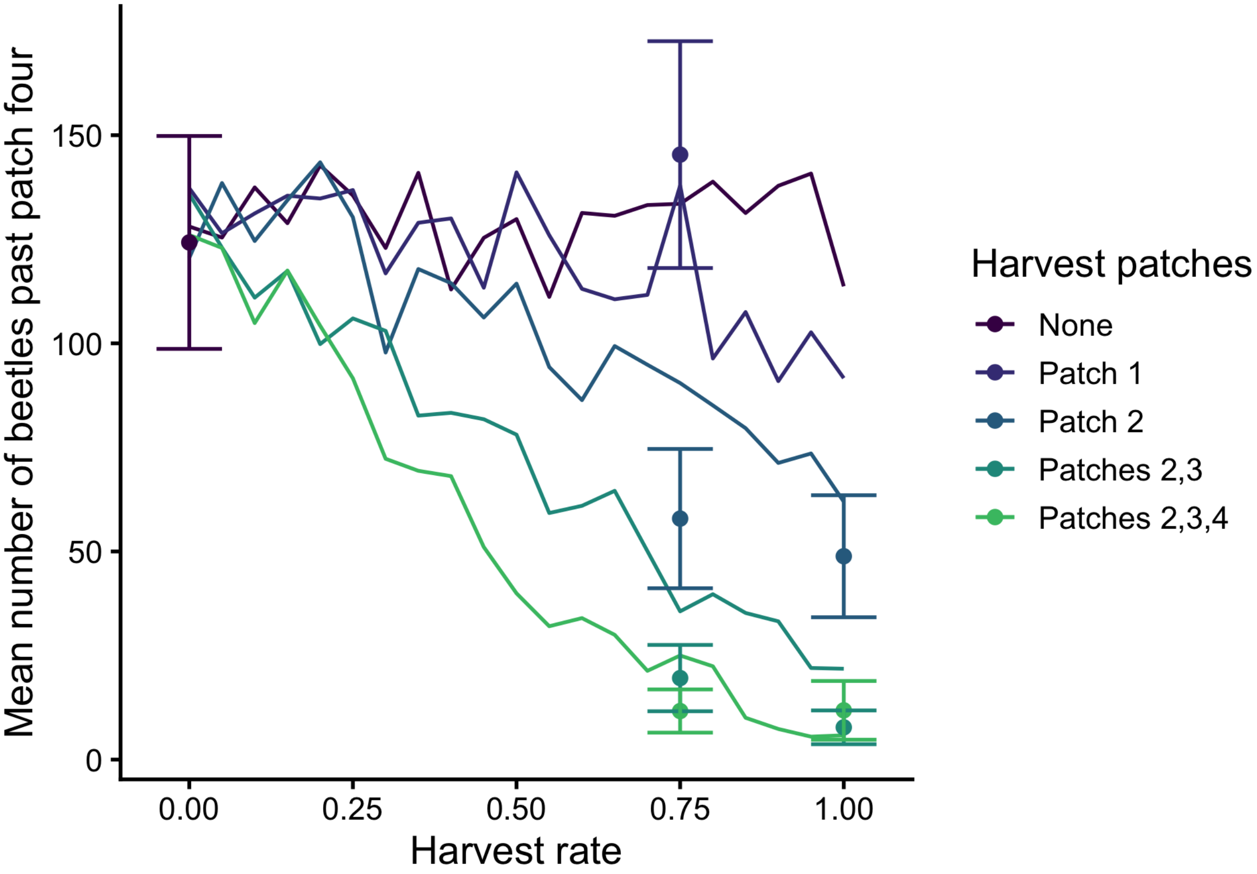

Figure 2: (a) Simulated (n=100 trials) mean total number adult beetles at the end of generation four and the (b) mean total number of beetles past patch four for various levels of harvesting in different barrier zones. Here, "Harvest Patches" refers to the specific patches where harvesting occured, e.g., 0 indicates no harvesting, 12 indicates harvesting in patches 1 and 2, etc.

to two or three patches did significantly reduce the population size and slow spread (Figs. 3,4). In general, increasing the barrier zone width appeared to have a larger effect on controlling population size and spread (Figs. 3,4), but this result was not very different for barrier zones with a width of two versus three patches.

We also found that management success depended strongly on the response variable. For example, controlling the total population size (Fig. 3) required a high degree of harvesting and a large barrier zone, i.e., a lot of management effort. The optimal management strategy depended on whether the objective was to keep numbers as low as possible or if another objective, such as maintaining the population below a threshold, was desired. Similarly, controlling the actual spatial spread, as opposed to population size, depended more on the barrier zone size than the harvesting rate (Fig. 4).

Despite the controlled experimental setting, the total population size and spatial spread varied within each treatment. We found that low effort management strategies led to the largest variability in responses (Fig. 5). The control, or no management, treatment had a 35% larger coefficient of variation in the total population size between treatments compared to the treatment with the highest management effort (Fig. 5). As another example of replicate and treatment variability, we examined the number of beetles during generation four in patch six, which represents the furthest a beetle could travel. Every treatment had a replicate that had some beetles in patch six, but every treatment also had a replicate that had zero beetles in patch six.

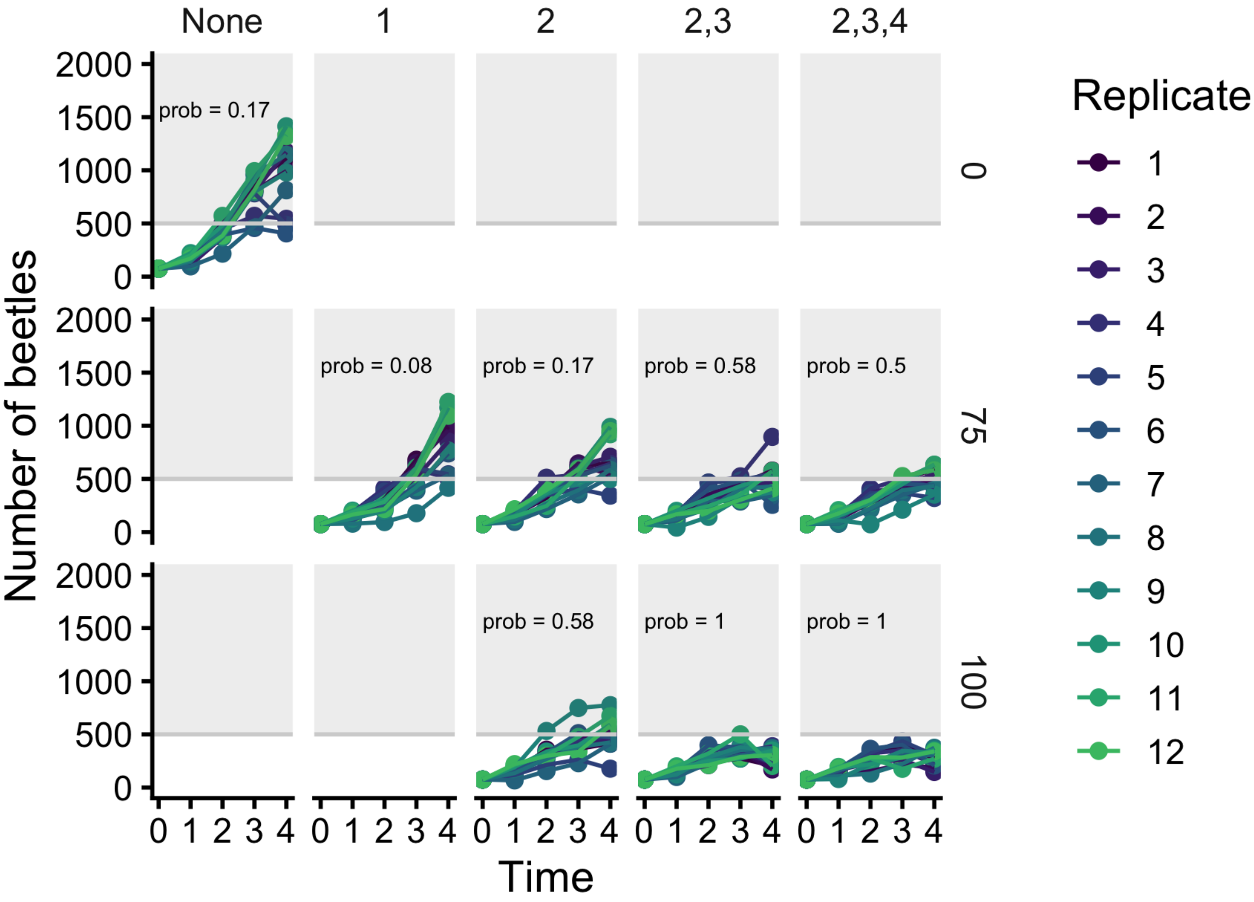

Figure 3: Total population size within each landscape over time for experimental replicates. Each subplot represents a different control strategy, with different levels of harvesting and patches in which harvesting took place (e.g., 2 versus 2, 3, and 4). The management objective (which was arbitrary) was to limit the population to less than 500 individual beetles. If a replicate passed into the indicated gray region, management was considered a failure. The barrier zone size, harvest rate, and generation time were all significant predictors ($P < 0.01$). Combined, these predictors explained 55% of the variation in successful management using a binomial error model (SI Appendix.

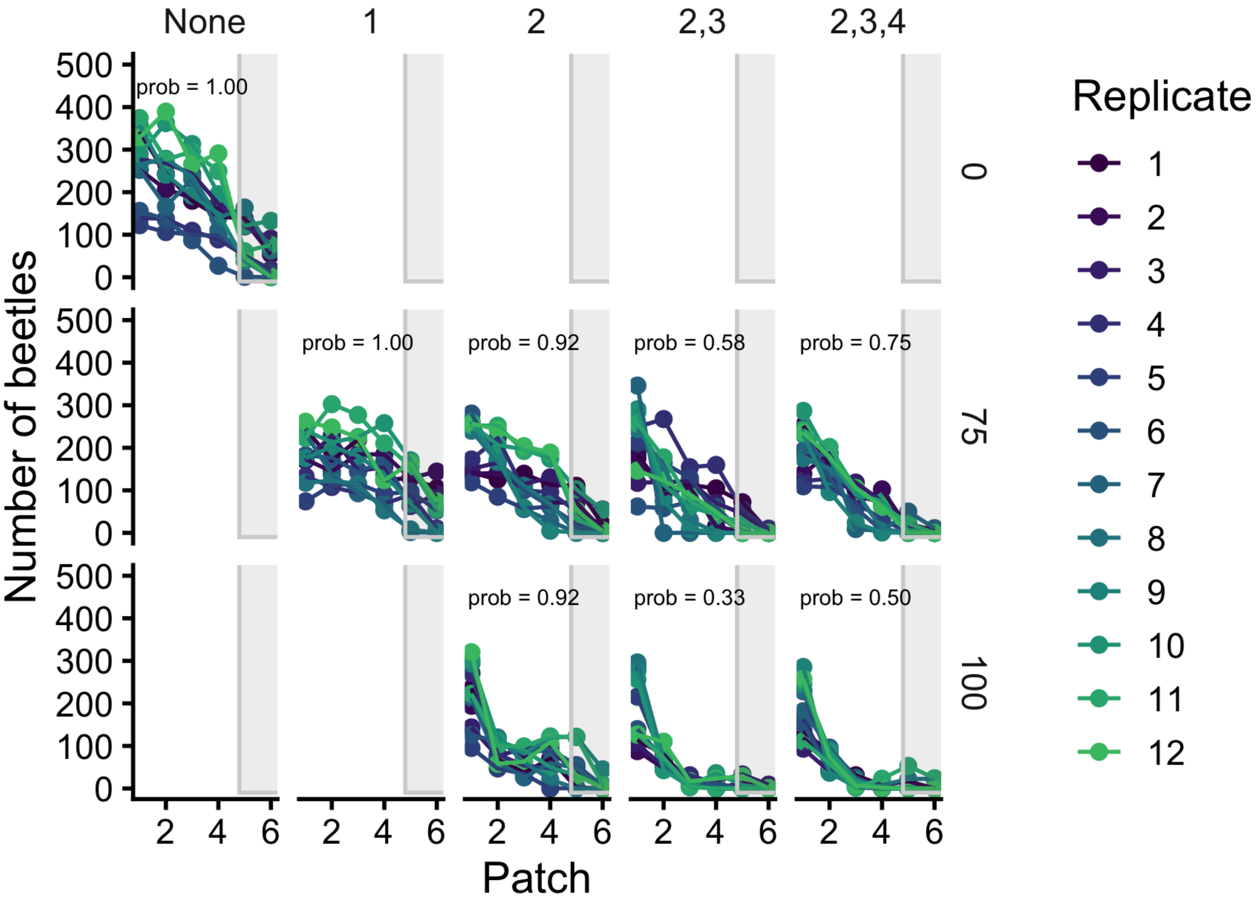

Figure 4: Population size by patch in generation four within each landscape. Each subplot represents a different control strategy, with different levels of harvesting and the patches in which harvesting took place (e.g., patch two versus patches two, three, and four). The management objective (which is arbitrary) was to limit the to not spreading beyond patch four. If a replicate passed into the indicated gray region, management was considered a failure. The barrier zone size, harvest rate, and generation time were all significant predictors ($P < 0.01$). Combined, these predictors explained 36% of the variation in successful management using a binomial error model (SI Appendix.

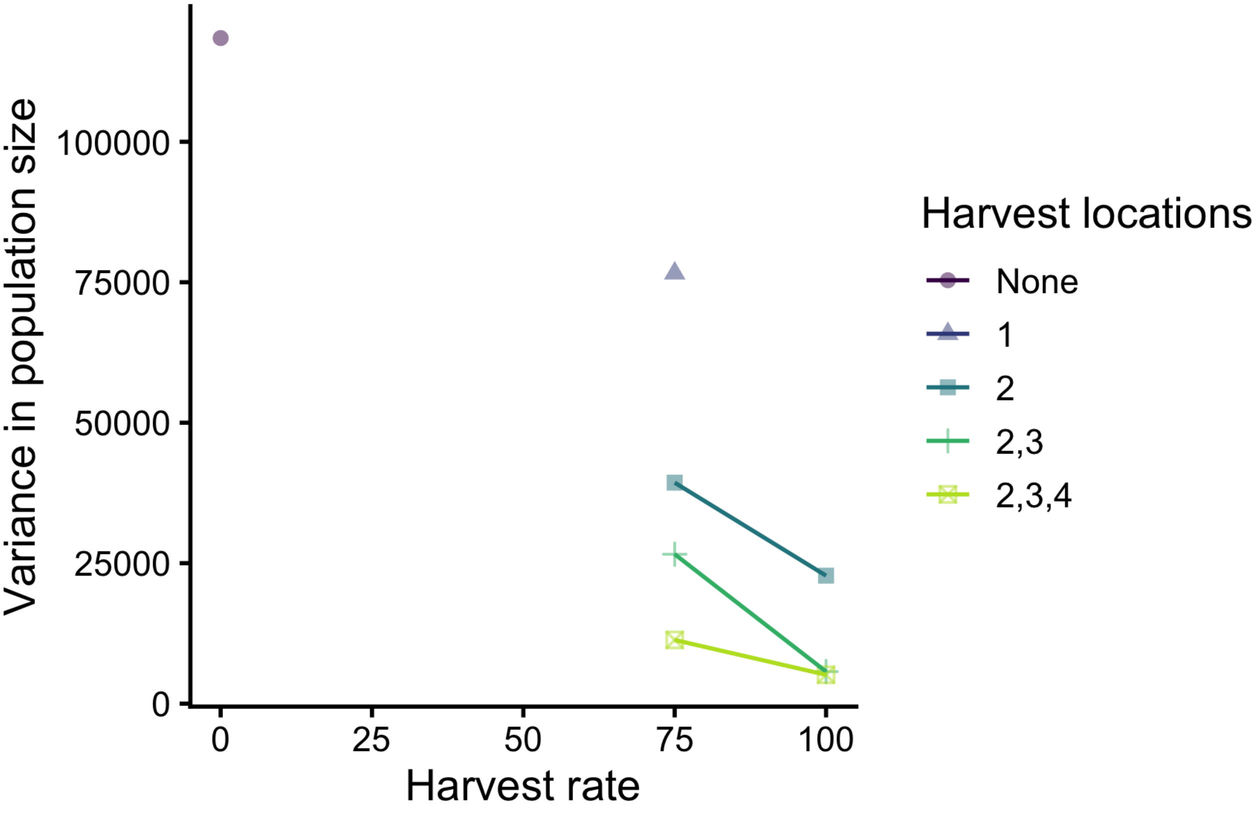

Figure 5: Variance in total population size between replicates during generation four.

Discussion

We used a mechanistic model and experimental microcosms to understand the effectiveness of barrier zones in controlling invasive species. We found that barrier zones can be an effective tool to control invasive species both in terms of population numbers and spatial spread (Figs. 2-4). Harvesting 75% in patch one without a barrier zone did little to stop the spread compared to the control with no harvesting (Figs. 2-4). Higher levels of harvesting and larger barrier zones were more effective control methods. However, the quantitative results were sensitive to dispersal rate assumptions, harvesting efficiency, and initial population density. These sensitivities highlight that general predictions about barrier zone success need to be interpreted with care.

Most of the empirical findings on barrier zones come from field implementations. For example, containment zones have been used to slow the spread of the Spongy moth in North America [Sharov & Liebhold 1998], while intensive harvest combined with barriers has been applied to contain invasive carp (Piczak et al. 2022). Invasive freshwater mussel containment in U.S. lakes has relied on similar principles, though usually in combination with chemical treatment and boat inspection programs (Angell et al. 2024, Haight et al. 2021). However, it is difficult to generalize from these field systems. A key warning from prior work is that both detection and harvesting of invasive species in the field are much more difficult compared to our perfectly controlled lab system. In addition, other management challenges have to be considered. For example, Myers et al. (1998) noted that "eliminating the last 1–10% of the population may demand equal expenditures of time, energy, and money to that required for the first 90–99% and therefore be more expensive per insect killed." Our experiments provide evidence for this idea, given that, even in the most intensive management scheme, a small number of beetles were still able to reach the end of the experimental landscapes.

Additionally, we found that the lowest control efforts, specifically small barrier zones and low harvesting, led to the most variable outcomes (Fig. 5). Both the total population size and the population size beyond the barrier zones were higher for these low-effort strategies. For example, the coefficient of variation for total population size was 30% higher for the small barrier zone and low harvesting treatment compared to the large barrier zone and high harvesting treatment (Fig. 5). This has important implications for how we interpret management outcomes in the field. If there is high variability in outcomes, there will also be high rates of false-positive and false-negative conclusions about any given control program. A low-effort strategy may appear successful simply by chance, especially when data is limited (White 2019, White and Bahlai 2021). Although theoretical models and other microcosm experiments have demonstrated such variability, it remains difficult to capture in field settings, since we often only have one "replicate" of an invasion. For instance, Spongy moth spread in the U.S. has been highly heterogeneous despite broadly similar control interventions, with some zones showing rapid establishment and others showing persistent suppression (slo 2002). Similar variability has been documented for quagga mussel spread across western lakes, despite uniform inspection protocols. Additional work using databases of invasive species spread (Suckling et al. 2019) may provide broader insight into variability in management outcomes.

Our work also highlights the management implications of the response variable choice and economic considerations. We found that the total population size in any treatment depended on both barrier zone size and harvest rate, whereas the population size beyond the barrier depended more on the barrier zone size (Tables S2-S3). This distinction emphasizes the importance of clearly defining goals within adaptive management frameworks (Walters and Holling 1990). For example, in sea lamprey management in the Great Lakes, the primary goal has often been framed in terms of damage reduction (number of preyed-upon fish), rather than total lamprey population size, leading to different control priorities (Grunder et al. 2021). Similarly, in agricultural systems, reducing crop damage rather than total pest abundance often drives control strategies (Babcock et al. 1992). The optimal strategy also depends on the relative costs of management versus damage. Although higher harvest rates and larger barrier zones were consistently more effective in our system, their optimality depends on whether the marginal reduction in damage outweighs the additional control costs. This tradeoff mirrors real-world debates in fisheries, forestry, and invasive species management (Epanchin-Niell and Hastings 2010).

The mathematical model captured the spatial spread well but generally overestimated population counts across treatments. Future work should explore whether this mismatch reflects limitations in parameterization or whether more complex models are needed. Our framework was specific to flour beetles; extensions could incorporate continuous spatial habitats, density-dependent reproduction, evolutionary dynamics, or rare long-distance dispersal events. Additional modeling approaches could include temporal variability (White and Hastings 2020) and how social acceptance of spatial management interacts with ecological dynamics (Baker-Médard et al. 2024, Wulfing and White 2024). Microcosm systems provide tractable opportunities to test these ideas before moving to the field. Future studies should also examine barrier zones in realistic field settings. For example, aquatic invasive species like carp are managed using electric dispersal barriers, but their long-term efficacy remains debated (Piczak et al. 2022). Furthermore, a better understanding of the variability in management outcomes will be especially important for adaptive management approaches. Ultimately, management success depends on how goals and costs are defined. Finding optimal eradication or containment strategies will become increasingly important as climate change accelerates invasion rates and expands the ranges of many species (Mainka and Howard 2010).

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Data and code availability

All data and code associated with this project is available at https://github.com/QuantMarineEcoLab/beetle-barrier-zones

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