Success and failure of ecological management is highly variable in an experimental test

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When managing natural systems, the importance of recognizing the role of uncertainty has been formalized as the precautionary approach. However, it is difficult to determine the role of stochasticity in the success or failure of management because there is almost always no replication; typically, only a single observation exists for a particular site or management strategy. Yet, assessing the role of stochasticity is important for providing a strong foundation for the precautionary approach, and learning from past outcomes is critical for implementing adaptive management of species or ecosystems. In addition, adaptive management relies on being able to implement a variety of strategies in order to learn—an often difficult task in natural systems. Here, we show that there is large, stochastically driven variability in success for management treatments to control an invasive species, particularly for moderate, and more feasible, management strategies. This is exactly where the precautionary approach should be important. Even when combining management strategies, we show that moderate effort in management either fails or is highly variable in its success. This variability allows some management treatments to, on average, meet their target, even when failure is probable. Our study is an important quantitative replicated experimental test of the precautionary approach and can serve as a way to understand the variability in management outcomes in natural systems which have the potential to be more variable than our tightly controlled system.

ecological management | stochasticity | adaptive management | invasive species

The need to confront uncertainty in management has been emphasized both generally (1, 2) and in the context of ideas like the precautionary principle (3) and adaptive management (4). Given this uncertainty, tools like structured decision making and evidence-based conservation are designed to improve management outcomes (5, 6). However, these tools can be difficult to use, as we often only have a single population to study and manage. A full understanding of the issues determining optimal management in the presence of stochasticity can be addressed with an experimental approach and replication.

The need to include stochastic aspects is particularly important in the control of invasive species, where there is often only a single successful invasion event, after which a species becomes established and continues to spread (7). Therefore, we lack information on both the probability of successful establishment and the variability in spatial spread. For example, lionfish in the Caribbean first appeared in the 1980s, but recently their populations have expanded rapidly (8). Whether local management actions to control lionfish fail or succeed, it will still be unclear if the outcome resulted from the management strategy chosen, its implementation, or stochasticity. To overcome issues of replication, trait-based risk assessments, meta-analyses, and mathematical models (9) can all be used to estimate probabilities of establishment and spread (7, 10, 11). A recently developed database of eradication programs shows the varying species responses to management (12). However, meta-analyses still suffer from study-design differences, environmental factors that differ between studies, and publication bias (13).

Experiments—more specifically, tightly controlled microcosms—provide replication and thus can properly quantify the role of stochasticity. These types of experiments can be used to address questions of general conservation concern (14). Fryxell et al. (15) used experimental microcosms of ciliates to understand how harvesting affected populations. They found that a fixed-quota harvesting policy led to the highest extinction risk. In a follow-up study, Fryxell et al. (16) found that reserves could prevent extinction of harvested populations. Even in these controlled laboratory settings, there was still variability in management outcomes. Similarly, work on invasive species showed that spatial spread can be highly variable, even across replicates with the same controlled laboratory conditions (17).

Despite the global importance of understanding invasive species, there is still limited empirical evidence on the effectiveness of different control-strategy combinations (18, 19). This is due, in large part, to the lack of replication (20). To control an invasive species, we implement a particular strategy, or set of strategies, in a single population. Suppose a combination of management actions fails; was it the wrong approach? The strategy could be the best approach, but, instead, natural variability led to failure. Suppose the strategy succeeds; could the same outcome have been achieved at a lower cost? With either success or

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Significance

From fisheries to invasive species, uncertainty plays a major role in management success or failure. The precautionary approach recognizes this, but there have been almost no experimental investigations of this issue due to a lack of replication for ecological management. We use a combination of mathematical models and experiments to show large variation in outcomes for invasive-species management. Our results provide a quantitative illustration of extreme variability in the success or failure of management strategies, particularly for optimal management strategies that try to maximize profits or minimize costs without proper consideration of stochasticity.

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failure, will the same outcome occur the next time a similar situation arises? This is a general set of problems in management (21). The success or failure of any management or conservation action depends on both the chosen action and implementation, but also the inherent variability present. This limits the effectiveness of adaptive management in the system (4).

We use both a microcosm experiment and stochastic population model (*SI Appendix*) to explore which strategy best controls the spread of an invading species. The model builds on an earlier model for the spatial stochastic dynamics of the flour beetle (*Tribolium castaneum*) (17, 22), which we parameterize (*SI Appendix*, Table S1 and Figs. S1–S3) for the related species, the confused flour beetle (*Tribolium confusum*). The model includes specific mechanisms (23) important for invasive species (e.g., dispersal and reproduction). Using the model, we choose a range of strategies close to the optimum and test the strategies experimentally. We then use the model retrospectively to study the variability in management outcomes both between and within treatments.

Results

With the parameterized model, we evaluated the effectiveness of 2 treatment strategies: harvesting of beetles in each patch and reducing dispersal (i.e., controlling the amount of time beetles are allowed to disperse between patches using plastic gates) (24). We then determined which combination of strategies either reduced population size to low levels or limited the spatial spread. There was large variability—not only between but also within treatments (Figs. 1 and 2). With a management objective to keep the population to less than 300 individuals, there was high predictability of management outcomes for low and high harvest rates (Fig. 1*A*). However, for intermediate harvest values, there was a probability of 0.50 of keeping the population to less than 300 individuals. To prevent spread past patch 3, either harvest rates had to be high enough, or, more importantly, dispersal times had to be low (Fig. 1*B*).

We tested our model predictions using a model insect, the confused flour beetle (*T. confusum*). *Tribolium* microcosms are an excellent model invasive species for 3 reasons. First, *Tribolium* microcosms have already been used to study spatial spread with corresponding stochastic population models (17, 22). Second, with microcosms, multiple replicates of the invasion process are possible (17, 25). This is in contrast to invasions in nature, which are rarely replicated. Lastly, *Tribolium* microcosms can be tightly controlled in the laboratory (*SI Appendix*, Fig. S1). This reduces other forms of error that can make differentiating between treatments difficult. Thus, microcosms can act as a control in comparison to natural systems, which are rarely perfectly observable (26). The specific control strategies of harvesting and limiting dispersal can also be controlled precisely.

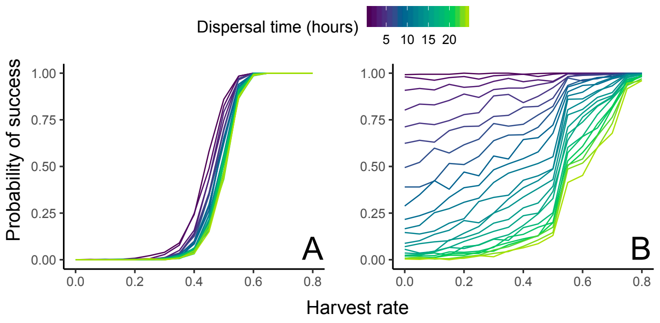

Fig. 1. Model predictions for management success. (*A*) Probability of successfully keeping the population to less than 300 individuals after 6 generations for different harvest rates and lengths of dispersal. (*B*) Probability of successfully preventing an invader from moving beyond patch 3 (of 6 total) after 6 generations for different harvest rates and lengths of dispersal. The curves are not smooth because the results come from stochastic simulations.

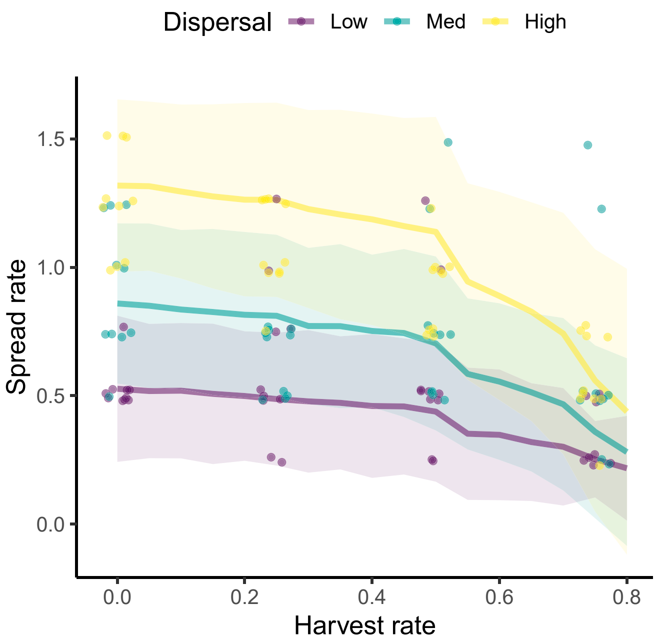

Fig. 2. Model predictions compared to experimental data for the spread rate of beetles in landscapes (number of patches colonized per generation). The solid lines represent the mean values from simulations. The shaded regions represent the 95% quantiles of the simulations. The simulations are for default parameter values (*SI Appendix*, Table S1). The filled circles represent data from the actual experiment. Spread rates of zero indicate extinction. The placement of points has been randomly perturbed to allow for visual clarity. Med, medium.

For each treatment, we censused the population each generation (Figs. 3 and 4 and Movie S1). In line with past work, there was variability in spread rates across, and within, treatments (Fig. 2). We found that population size and number of patches invaded decreased with increased harvesting rate or decreased dispersal time (Figs. 2–4). After only 6 generations, we found clear differences between treatments. There was also an interaction effect between the harvesting and dispersal control strategies; higher harvest rates were particularly effective with high levels of dispersal (Fig. 2 and *SI Appendix*, Table S3).

Because of the variability in spread rates, there was also variability in management outcomes. With a management goal of reducing population size, if there was no harvest, or if harvest rates were high, management outcomes were not variable, with 100% of the replicates failing, or accomplishing, the objective (Fig. 3 and *SI Appendix*, Table S2 and Fig. S4). At intermediate levels of harvesting, and particularly at low levels of dispersal, management outcomes were more variable, with success rates ranging between 0 and 62% (Fig. 3). Another objective was to limit the spatial spread, as opposed to population size, of the beetles. Here, again, there was variability in management outcomes (Fig. 4 and *SI Appendix*, Table S3). This was particularly true for intermediate values of harvesting, with success rates between 10 and 100% (Fig. 4).

Discussion

Combined, these results highlight an important message about species management. Even in tightly controlled microcosms, there was still significant variability in management outcomes. This occurs even in a system where we have a very detailed, parameterized simulation model—a challenging task in most

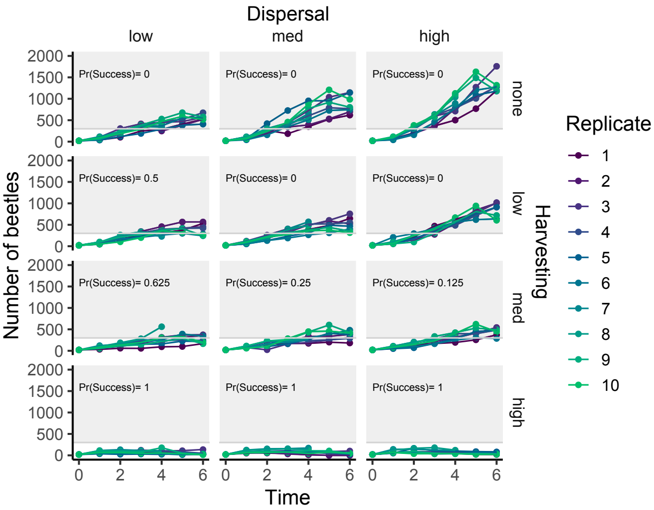

Fig. 3. Total population size within each landscape over time for experimental replicates. Each subplot represents a different control strategy, with different levels of dispersal or harvesting. The management objective was to limit the population to less than 300 individual beetles. If a replicate passed into the indicated gray region, management was considered a failure. The probability of success (fraction of replicates within a treatment with less than 300 beetles in generation 6) is shown for each treatment. Dispersal, harvesting, and generation time were all significant predictors ($P < 0.01$). Combined, these 3 predictors explained 69% of the variation in successful management using a binomial error model (*SI Appendix*, Table S2). Med, medium.

natural systems (1). This shows the difficulty in evaluating management programs and ultimately implementing adaptive management (4). The effectiveness of a management program depends on the control strategy chosen, implementation, and stochasticity. Variability in management outcomes led to situations where, on average, a control strategy met the objective, but was still most likely to fail. For example, when dispersal was high with a medium amount of harvesting, on average, the treatment achieved the target reduction in limiting spatial spread; yet, the probability of success was only 40% (Fig. 4).

The levels of variability in management outcomes also depend on species life history and the specific control strategy used (Figs. 3 and 4 and *SI Appendix*, Figs. S5 and S6). This is in line with past work using mathematical models or meta-analyses focused on common characteristics (trait-based) of invasive species. (7, 11, 27). In our experiment, a population with high dispersal rates (i.e., low levels of control on dispersal) produced the most variability in management outcomes (Figs. 3 and 4). Importantly, we show that the variability in management outcomes depends on the specific harvest and dispersal-control strategies used. Moderate levels of harvest and dispersal were the most susceptible to highly variable management outcomes. This is concerning for managing natural systems, as it is often impossible to implement management strategies with such effectiveness. Thus, we would expect that most real-life management programs would experience large variability, and less predictability, in their outcomes. The large variability in outcomes would also necessitate an adaptive management approach that was adjusted to the specific state of the system.

Another way to view the highly variable outcomes is that these occur when the control strategy is close to what would be the minimum effort or cost needed to control spread, on average. Thus, these results illustrate the importance of what in similar contexts has been called the precautionary approach (3). Just as in fisheries where harvest below the deterministic optimum at a potential cost in average profit can be important in long-term sustainability, here, spending a bit more on control than what is needed to guarantee success on average can make success much more likely.

More generally, there has been little work done on understanding variability in management outcomes. This is largely because natural systems typically lack replication, or replication is only available in the context of recurrent decision problems, which provides only temporal replication. Yet, implementing adaptive management relies on replication within and across management treatments (4, 19). Agricultural experiments are often replicated enough to understand the variability for a particular management action. For example, Smith et al. (28) examined the effect of different agricultural-management strategies on crop-yield variability. They found that there was much variability both within and between treatments. Other work has suggested that microcosms could be used to better understand problems of global concern (14). With this in mind, our work addresses the variability in management outcomes for invasive-species control. Fryxell et al. (15) did not examine invasive species, but instead evaluated the effect of different harvest strategies in ciliate *Tetrahymena thermophila* microcosms. They found that population variability was greatest for a fixed-quota harvest strategy. These results, combined with our findings, highlight the variability in potential outcomes for any one management strategy. Furthermore, our experiment was in conducted in a highly controlled, laboratory setting. In natural systems, even larger variability in management outcomes might be expected.

Our study should be extended in several important ways. Natural variation in dispersal or growth rates from year to year could increase uncertainty of success when controlling spatial spread. Also, we examined only a single species, but in many systems, species interactions are important in the context of invasive species (18, 29, 30). Additionally, because we used a microcosm system, there were no explicit costs or benefits to managing our populations. In a real system, determining these

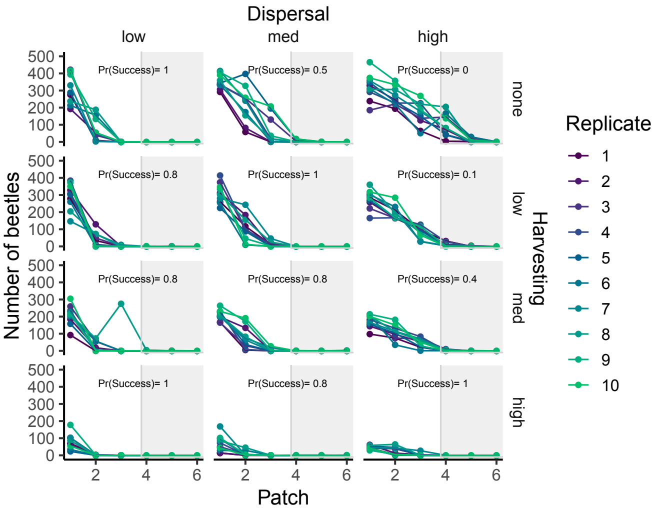

Fig. 4. Population size in each patch within each landscape for generation 4 for experimental replicates. Each subplot represents a different control strategy, with different levels of dispersal or harvesting. The management objective was to prevent spread past patch 3. If a replicate passed into the indicated gray region, management was considered a failure. The probability of success (fraction of replicates within a treatment with no beetles past patch 3) is shown for each treatment. Dispersal, generation time, and the interaction between harvesting and dispersal were all significant predictors ($P < 0.01$). Combined, these 3 predictors explained 40% of the variation in successful management using a binomial error model (*SI Appendix*, Table S3). Med, medium.

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costs and benefits is crucial when selecting an optimal control strategy (26, 31–33). Issues of management costs are especially important when using multiple strategies in tandem—like population harvesting and controlling dispersal (34). This was particularly relevant in our experiment, where there was a clear interaction effect between our management strategies (Fig. 2 and *SI Appendix*, Table S3). Our experiment also presents an ideal approach to compare human- and model-based strategies of managing ecosystems (35, 36). Past work, in less-realistic, computer-simulated studies, has shown that predictions from models were similar to subjective judgement, but there was more bias with subjective judgement (35). Thus, more realistic, but still replicated, microcosm systems can be used to test and compare different approaches to management, while also accounting for costs and benefits explicitly.

Further work in natural systems is needed to evaluate the variability in management outcomes (1). In particular, it would be beneficial to understand the strongest predictors of management variability. This would ultimately determine the level of predictability and confidence we can have in a management program. We can then use decision-science tools, like stochastic dynamic programming, to manage in the face of this uncertainty (37). We hope our study inspires future empirical and theoretical analysis on the variability in ecological management outcomes.

Materials and Methods

Experimental Design. We obtained confused flour beetles (*T. confusum*) from stock populations maintained in 4- × 4- × 6-cm containers with 30 mL of flour and yeast medium. We set up 6-patch landscapes connected by a small dispersal channel (2-mm diameter). We filled each patch with 20 g of standard medium (95% flour and 5% brewer's yeast). We maintained populations within incubators at 31 (± 0.2 SD) °C and 52 (± 4.5 SD) % relative humidity (*SI Appendix*, Fig. S1).

On day 1, we inoculated patch 1 with 20 individual adult beetles. These beetles were allowed to lay eggs (with no dispersal allowed) for 24 h. Adult beetles were then removed from each patch by using a sieve. On day 41, we allowed adult beetles to disperse for a set number of hours. We controlled dispersal time by closing and opening gates (plastic screens) that were placed between patches. On day 42, we censused the number of adult beetles. Then, we placed a fraction of adults in fresh medium. The fraction of adults was set by a harvesting function. There are many different possible harvesting strategies (38). We chose a fixed-proportion strategy (a fraction of beetles were harvested from every patch each generation) for its simplicity. 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. We then had adult beetles lay eggs for 24 h before being removed.

We used a 4 × 3 factorial design to test the effects of harvesting and dispersal on invasive-species management. We had harvest rates of zero ($H = 0$), low ($H = 0.25$), medium ($H = 0.5$), and high ($H = 0.75$). We examined 3 levels of dispersal: 1, 6, or 24 h per generation. This design resulted in 12 different landscape treatments (including a control with no harvesting and 24 h of dispersal). To ensure high statistical power (39), we replicated each treatment 10 times for a total of 120 landscapes (720 total patches), and we ran the experiment for 6 generations (36 wk).

We used a generalized linear model with a binomial error structure (and logit link function) to determine the probability of success or failure for each management strategy. Predictor variables were the levels of harvesting and dispersal, their interaction, and generation (*SI Appendix*, Tables S2 and S3). We examined residuals from the models for normality and homogeneity assumptions.

Dispersal Experiment. We conducted additional experiments where we varied the time of dispersal to estimate parameters for a dispersal kernel to be used in the full stochastic model. We placed 75 adult beetles in patch 1 of a landscape. We let them lay eggs for 24 h and then removed them. Beetles were allowed to develop for 41 d before the gates were opened to allow dispersal. Gates were open for either 1, 6, 12, 24, or 48 h. Each patch was then censused to see how far beetles moved (*SI Appendix*, Fig. S2).

Previous work designed a similar dispersal experiment to parameterize dispersal kernels in a population model (17). They found that a Poisson dispersal kernel with extra variation given by a Dirichlet-multinomial distribution was the best-fitting dispersal kernel for the related species *T. castaneum*. Thus, we fit our dispersal experiment data to parameterize the same dispersal kernel (equations 2, 3, and 7 in the supplement to ref. 17). Using maximum-likelihood estimation, we found that $D = 0.38$ and $s = 46.32$ (*SI Appendix*, Table S1).

Recruitment Experiment. We inoculated individual patches with different starting densities of adult beetles. They were allowed to lay eggs for 24 h, and then the adults were removed by using a sieve. At the end of 6 wk, we censused beetles in line with the methods described in the main experiment (*Experimental Design*). In total, we had 5 replicates for each of the following densities: 2; 4; 8; 16; 32; 64; 100; 150; 300; 500; 750; and 1,000. We also included an additional 59 replicates of an initial beetle density of 75 from the experiment on fitting the dispersal functions. We then compared the density after 1 generation to the initial densities (*SI Appendix*, Fig. S3).

Melbourne and Hastings (22) parameterized a family of stochastic Ricker functions for a similar species, *T. castaneum*. They found that the most detailed model (including demographic stochasticity, stochastic sex determination, environmental stochasticity, and demographic heterogeneity) was the best-fitting model. We used this negative binomial–binomial–gamma Ricker model (for model equations, see p. 5 and table 1 in the supplement to ref. 22) and fit it to our data by using maximum likelihood.

Data Availability. All of the data and code used in this manuscript are available at https://github.com/eastonwhite/species-management-variability (40).

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