



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

Easton R. White^{a,b,1}, Kyle Cox^c, Brett A. Melbourne^d, and Alan Hastings^{c,e}

^aDepartment of Biology, University of Vermont, Burlington, VT 05405; ^bCenter for Population Biology, University of California, Davis, CA 95616; ^cDepartment of Environmental Science and Policy, University of California, Davis, CA 95616; ^dDepartment of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309; and ^eSanta Fe Institute, Santa Fe, NM 87401

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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

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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Data deposition: All of the data and code used in this manuscript are available at <https://github.com/eastonwhite/species-management-variability>.

¹To whom correspondence may be addressed. Email: eastonwhite@gmail.com.

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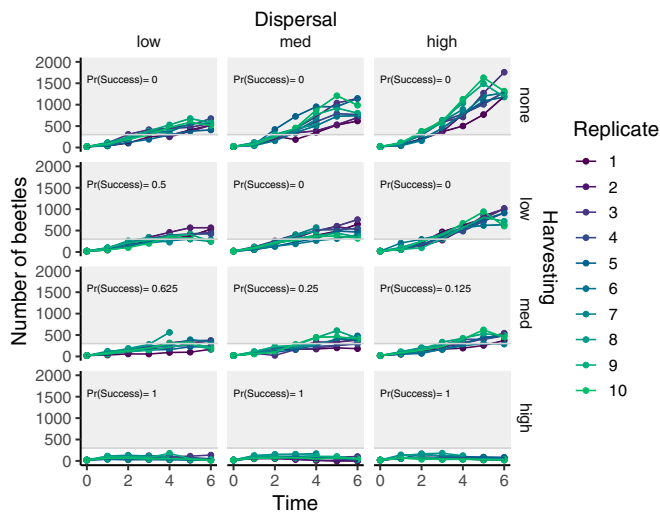


Fig. 3. Total population size within each landscape over time for experimental replicates. Each subplot represents a different control strategy, with different levels of dispersal or harvesting. The management objective was to limit the population to less than 300 individual beetles. If a replicate passed 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 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

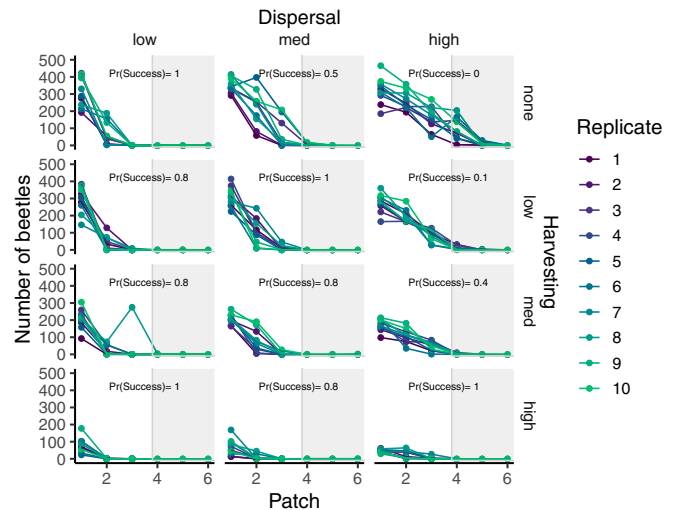


Fig. 4. Population size in each patch within each landscape for generation 4 for experimental replicates. Each subplot represents a different control strategy, with different levels of dispersal or harvesting. The management objective was to prevent spread past patch 3. If a replicate passed into the 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.

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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- M. A. McCarthy, Contending with uncertainty in conservation management decisions. *Ann. NY Acad. Sci.* **1322**, 77–91 (2014).
- E. J. Milner-Gulland, K. Shea, Embracing uncertainty in applied ecology. *J. Appl. Ecol.* **54**, 2063–2068 (2017).
- C. J. Walters, Is adaptive management helping to solve fisheries problems? *Ambio* **36**, 304–307 (2007).
- M. J. Westgate, G. E. Likens, D. B. Lindenmayer, Adaptive management of biological systems: A review. *Biol. Conserv.* **158**, 128–139 (2013).
- W. J. Sutherland, A. S. Pullin, P. M. Dolman, T. M. Knight, The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305–308 (2004).
- M. W. Schwartz *et al.*, Decision support frameworks and tools for conservation. *Conserv. Lett.* **11**, 1–12 (2018).
- D. M. Lodge *et al.*, Risk analysis and bioeconomics of invasive species to inform policy and management. *Annu. Rev. Environ. Resour.* **41**, 453–488 (2016).
- M. A. Albins, M. A. Hixon, Worst case scenario: Potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ. Biol. Fish.* **96**, 1151 (2013).
- J. M. Drake, D. M. Lodge, Allee effects, propagule pressure and the probability of establishment: Risk analysis for biological invasions. *Biol. Invasions* **8**, 365–375 (2006).
- A. M. Liebhold *et al.*, Eradication of invading insect populations: From concepts to applications. *Annu. Rev. Entomol.* **61**, 335–352 (2016).
- G. M. Palamara, F. Carrara, M. J. Smith, O. L. Petchey, The effects of demographic stochasticity and parameter uncertainty on predicting the establishment of introduced species. *Ecol. Evol.* **6**, 8440–8451 (2016).
- J. M. Kean *et al.*, Global eradication and response database. <http://b3.net.nz/gerda>. Accessed 28 April 2019.
- J. Koricheva, J. Gurevitch, Uses and misuses of meta-analysis in plant ecology. *J. Ecol.* **102**, 828–844 (2014).
- T. G. Benton, M. Solan, J. M. J. Travis, S. M. Sait, Microcosm experiments can inform global ecological problems. *Trends Ecol. Evol.* **22**, 516–521 (2007).
- J. M. Fryxell, I. M. Smith, D. H. Lynn, Evaluation of alternate harvesting strategies using experimental microcosms. *Oikos* **111**, 143–149 (2005).
- J. M. Fryxell, D. H. Lynn, P. J. Chris, Harvest reserves reduce extinction risk in an experimental microcosm. *Ecol. Lett.* **9**, 1025–1031 (2006).
- B. A. Melbourne, A. Hastings, Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. *Science* **325**, 1536–1539 (2009).
- A. Lampert, A. Hastings, E. D. Grosholz, S. L. Jardine, J. N. Sanchirico, Optimal approaches for balancing invasive species eradication and endangered species management. *Science* **344**, 1028–1031 (2014).
- R. Serrouya *et al.*, Saving endangered species using adaptive management. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 6181–6186 (2019).
- Y. M. Buckley, Predicting invasion winners and losers under climate change. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 4040–4041 (2017).

21. E. T. Game, P. Kareiva, H. P. Possingham, Six common mistakes in conservation priority setting. *Conserv. Biol.* **27**, 480–485 (2013).
22. B. A. Melbourne, A. Hastings, Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**, 100–103 (2008).
23. M. C. Urban *et al.*, Improving the forecast for biodiversity under climate change. *Science* **353**, 1113 (2016).
24. J. Blackwood, A. Hastings, C. Costello, Cost-effective management of invasive species using linear-quadratic control. *Ecol. Econ.* **69**, 519–527 (2010).
25. M. L. Vahsen, K. Shea, C. L. Hovis, B. J. Teller, R. A. Hufbauer, Prior adaptation, diversity, and introduction frequency mediate the positive relationship between propagule pressure and the initial success of founding populations. *Biol. Invasions* **20**, 2451–2459 (2018).
26. T. M. Rout, J. L. Moore, M. A. McCarthy, Prevent, search or destroy? A partially observable model for invasive species management. *J. Appl. Ecol.* **51**, 804–813 (2014).
27. K. M. Kettenring, C. R. Adams, Lessons learned from invasive plant control experiments: A systematic review and meta-analysis. *J. Appl. Ecol.* **48**, 970–979 (2011).
28. R. G. Smith, F. D. Menalled, G. P. Robertson, Temporal yield variability under conventional and alternative management systems. *Agron. J.* **99**, 1629–1634 (2007).
29. Y. M. Buckley, Y. Han, Managing the side effects of invasion control. *Science* **344**, 975–977 (2014).
30. E. S. J. Rauschert, K. Shea, Competition between similar invasive species: Modeling invasional interference across a landscape. *Popul. Ecol.* **59**, 79–88 (2017).
31. R. S. Epanchin-Niell, A. Hastings, Controlling established invaders: Integrating economics and spread dynamics to determine optimal management. *Ecol. Lett.* **13**, 528–541 (2010).
32. A. L. Moore, M. A. McCarthy, On valuing information in adaptive-management models. *Conserv. Biol.* **24**, 984–993 (2010).
33. J. Firn *et al.*, Priority threat management of invasive animals to protect biodiversity under climate change. *Glob. Chang. Biol.* **21**, 3917–3930 (2015).
34. A. Lampert, A. Hastings, How to combine two methods to restore populations cost effectively. *Ecosphere* **10**, e02552 (2019).
35. M. A. McCarthy *et al.*, Comparing predictions of extinction risk using models and subjective judgement. *Acta Oecol.* **26**, 67–74 (2004).
36. M. H. Holden, S. P. Ellner, Human judgment vs. quantitative models for the management of ecological resources. *Ecol. Appl.* **26**, 1553–1565 (2016).
37. I. Chadès *et al.*, Optimization methods to solve adaptive management problems. *Theor. Ecol.* **10**, 1–20 (2017).
38. C. M. J. Strevens, M. B. Bonsall, The impact of alternative harvesting strategies in a resource-consumer metapopulation. *J. Appl. Ecol.* **48**, 102–111 (2011).
39. E. R. White, Minimum time required to detect population trends: The need for long-term monitoring programs. *BioScience*, **69**, 40–46 (2019).
40. E. R. White, Species management variability. GitHub. <https://github.com/eastonwhite/species-management-variability>. Deposited 9 September 2019.