Control effort exacerbates invasive-species problem

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Abstract. Ecosystem managers face a difficult decision when managing invasive species. If they use aggressive practices to reduce invader abundances, they will likely reduce invaders' competitive impacts on natives. But it is often difficult or impossible to reduce invaders without damaging natives. So a critical question becomes: Which is worse for native biota, invaders or things done to control invaders? We attempted to answer this question for a common scenario. We studied several grassland natives exhibiting long-term coexistence with an invader and asked how aggressive management (herbicide use) affected the natives. Whether or not grazing was excluded, one-time herbicide use made two native forbs exceedingly rare for our entire 16-year study period. Herbicide also made several other native forbs rare, but only when grazing was excluded, and there is evidence that the dominant invader became more abundant in response to the decreases in native-forb abundances. Throughout the world, terrestrial and aquatic ecosystems are receiving herbicide applications for exotic-species control. Some of the applications are doubtless warranted because they target small invader patches or larger areas with virtually no remaining natives. However, other herbicide applications occur where large native populations occur, and our data suggest that these applications can be ill advised. Our cautionary tale is told using an herbicide-treated grassland, but our results should be considered wherever invasive-species management damages native species.

Key words: Bayesian; Euphorbia esula; grasslands; herbicide use for invasive species; invasive species; leafy spurge; Montana (USA) rangelands; native species.

INTRODUCTION

Unassailable evidence implicates exotic species in globally declining biodiversity (Wilcove et al. 1998, Pimentel et al. 2005). Yet many native biota seem to be persisting indefinitely alongside some of the world's most tenacious invaders. In some cases, native prairie plants are persevering beneath dense exotic-plant canopies (Lesica and Hanna 2004), native fish have not expired even under intense competition from extraordinary abundant exotic-fish competitors (Bunnell 2006), and native butterflies maintain populations as multiple invaders parasitize them, displace their food, and compete with them for what food remains (Keeler et al. 2006).

That invasive species so often imperil natives without outright extirpating them begs a precautionary approach to ecosystem management. Specifically, once invaders render natives rare, avoiding practices that might further rarify them can very clearly seem the prudent course of action. However, the prudent course of action can become less clear with management

Manuscript received 7 September 2007; revised 23 April 2008; accepted 6 May 2008. Corresponding Editor: S. K. Collinge.

practices used explicitly for suppressing invaders. On one hand, these practices often do have negative side effects on native species. For example, the pesticides and traps used to control exotic-fish also impact native fish and amphibians (Fontenot et al. 1994), and introduced biological agents sometimes attack natives in addition to attacking exotic targets of intent (Kimberling 2004). On the other hand, these negative effects may be outweighed by positive effects on native species because natives often rebound when management suppresses invaders (e.g., Kennedy et al. 2005, Coleman and Levine 2007). In summary, invasive-species management can have both positive and negative consequences for native species, and in light of these conflicting consequences it is sometimes difficult to know a priori whether management will make matters better or worse.

Herbicides are one of several management tools capable of harming native species in addition to harming exotic targets, and these chemicals were the focus of our study. Some herbicides used in natural areas, such as glyphosate, are phytotoxic to the vast majority of species, both native and nonnative (e.g., Cosgriff et al. 2004). Others, such as 2,4-D and picloram, are highly toxic only to dicotyledonous species, but these chemicals are widely used where native and exotic dicots co-occur (e.g., Lym and Messersmith 1994, Wagner et al. 2007).

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Natural-area spraying is not tracked consistently, making it difficult to reasonably estimate global hectares sprayed. A few U.S. agencies do track their herbicide use, and, collectively, the U.S. Bureau of Land Management, Forest Service, and Park Service spray over 120 000 ha of natural area each year (Cota 2004, Exotic Plant Management Team 2006; R. Lee, *personal communication*).

We applied dicot-specific herbicide treatments (i.e., herbicide, no herbicide) to a grassland with relatively abundant monocots (i.e., grasses) and exotic dicots (forbs), and relatively rare native dicots (forbs, a subshrub, and a shrub). In factorial combination with the herbicide treatments we applied grazing treatments (i.e., cattle grazing, no cattle grazing). We gathered data intermittently for 16 years following herbicide application. Our primary objective was to evaluate nativespecies responses to herbicide and grazing treatments. We hoped these treatment responses might indicate something general about invasive-species management. Specifically, what are plausible native-species responses when management harms invaders and natives alike?

Methods

We conducted our study on an alluvial-fan grassland site residing on a cattle ranch near Grass Range, Montana, USA (see Plate 1). The site's grasses included a mix of natives such as *Pascopyrum smithii* and *Stipa viridula* and nonnatives such as *Agropyron cristatum* and *Poa pratensis*. The site's non-grasses included several native and nonnative forbs, which are discussed in the *Results* section, below.

By far the site's most abundant forb was Euphorbia esula, an exotic invader infesting millions of U.S. hectares (Duncan et al. 2004). E. esula was so abundant that an attempt was once made to kill the weed with herbicide, with the underlying goals being to increase grass forage for cattle and restore native-plant populations on the ranch. The herbicide used was picloram, a growth regulator that injures or kills a wide range of forbs and other dicotyledonous plants while usually having little or no effect on grasses or other monocotyledonous species. Unlike herbicides that damage plants only following foliar contact (e.g., glyphosate), picloram can also damage plants following uptake from soil. Picloram can also curtail seed germination (Carrithers et al. 2005). In June 1982 a fixed-wing aircraft applied picloram to the site at a typical grassland-use rate (i.e., 1.1 kg/ha). About 800 ha were treated, with our study plots residing near the center of this large treated area.

Our study consisted of twelve 12×20 -m plots each of which received one of the following treatments: (1) cattle grazing, (2) herbicide, (3) both cattle grazing and herbicide, or (4) neither cattle grazing nor herbicide. These four treatments were arranged in a block design with three replications. Tarps were laid down shortly before spraying to prevent spraying of not-sprayed plots, while fencing was used to prevent cattle from grazing not-grazed plots. Cattle grazing over the study period occurred in the summer, and because our study site was on a working cattle ranch, specific timings, frequencies, and intensities of grazing were at the discretion of the ranch manager. Roughly, grazing was in accordance with the "take half leave half" principle that guides grazing management decisions on many western U.S. rangelands.

We visually estimated percentage plant cover of each species independently, except for grasses, which we estimated as a group. Initially, cover data were gathered one month and one, two, and four years after herbicide application. Then, after realizing the grazing exclosures were still intact, we gathered data again 16 years after application. Within each plot, cover was estimated near the time of peak standing crop in five 20×50 -cm frames that were spaced 1.5 m apart along each of two transects (2 transects × 5 frames = 10 frames per plot per year). Our measurement scheme ensured cover was estimated at fixed locations throughout the study period, which controlled for small-scale spatial variation and thereby increased our ability to detect change.

In addition to estimating cover, we estimated *E. esula* and grass biomass production during the herbicide application year as well as one 1, 2, 4, and 16 years after application. In each plot, biomass was clipped from five randomly placed 0.5×1.0 m frames around the time of peak standing crop. Clip height was 3.0 cm above the soil surface, and areas clipped in a given year were excluded from subsequent sampling later in the study. Current year's growth was extracted from the biomass samples and this material was sorted by plant group. The samples were dried at 50°C for 48 h and weighed.

ANALYSIS

Cover and frequency analysis

We addressed the following questions with our cover data: (1) Did the native species recover from herbicide use? and (2) To what extent did grazing influence the recovery of natives? To answer these questions, we restricted our analysis to data collected 4 and 16 years after herbicide application. We excluded data from one to three years post-herbicide application because most dicot species were completely absent from herbicidetreated plots during these years, probably because herbicide was still present at phytotoxic concentrations.

Some natives were absent from most cover-sampling frames, so our cover data set contained many zeros. This prevented the likelihood function for the data from being well approximated by a normal distribution. Therefore, we graphed the cover data by treatment in hopes of identifying an alternative analytical approach. The main conclusion from the graphs was that, given that a species was present in a frame, its cover in that frame was not appreciably affected by spraying. Otherwise stated, herbicide sometimes affected the number of frames a species occupied but if a species was present in a frame its cover in that frame was not appreciably affected by herbicide.

The finding that herbicide did not greatly affect cover within occupied frames allowed for an analysis based on the binomial distribution. Without substantial loss of information, we coded species as present or absent from sampling frames. In some cases we grouped taxonomically similar species because it was difficult to distinguish between them in the field. We also grouped three species that were individually too rare to conform to our statistical model, and hereafter we refer to this group as the "sparse forbs." Within plot *i*, year *j*, we assumed the number of frames occupied by a given species or species group (y_{ij}) was binomially distributed:

$$p(\mathbf{y}_{ij}|\boldsymbol{\beta},\boldsymbol{\sigma}) = \begin{pmatrix} 10\\ \mathbf{y}_{ij} \end{pmatrix} \left(\frac{e^{\eta_{ij}}}{1+e^{\eta_{ij}}} \right)^{\mathbf{y}_{ij}} \left(\frac{1}{1+e^{\eta_{ij}}} \right)^{10-\mathbf{y}_{ij}}$$
(1)

where $\eta_{ij} = \ln(\mu_{ij}/(1 - \mu_{ij}))$ and μ_{ij} is the probability of observing a species of interest in one of 10 plot *i*, year *j* sampling frames. We assumed the η_{ij} followed a normal linear model:

$$\eta_{ij} = (\mathbf{X}\beta)_{ij} + \varepsilon_{ij} \tag{2}$$

where **X** is a predictor variable matrix, $\boldsymbol{\beta}$ is a vector of fixed effects describing influences of various factors (i.e., replications, years, grazing, herbicide, interactions), and $\varepsilon_{ij} \sim \mathcal{N}(0, \sigma^2)$. In order to control for potential autocorrelations among repeated measurements of plots, we also evaluated plot-specific random effects in Eq. 2. However, we ended up excluding these random effects because they did not appreciably alter our results.

From a Bayesian perspective, Eqs. 1 and 2, respectively, form the prior distribution and likelihood function for the η_{ij} . To complete our hierarchical Bayesian model, we assigned a commonly used noninformative prior distribution to $\boldsymbol{\beta}$ and σ^2 :

$$p(\boldsymbol{\beta}, \sigma^2 | \mathbf{X}) \propto \sigma^{-2}.$$

See Chapter 16 of Gelman et al. (2004) for more details on this kind of model. We used Markov chain Monte Carlo (MCMC) integration to simulate the joint posterior distribution of model parameters for each species. We wrote a Fortran program to perform the integrations (Intel Corporation 2003).

Eq. 2 could potentially contain large numbers of treatment and interaction parameters, while our data set was not large enough to reliably estimate all these parameters. It was therefore useful to exclude parameters lacking substantial explanatory power. To identify unnecessary parameters, we relied on graphical posterior predictive checks (Gelman et al. 2004) and the deviance information criterion (DIC; Spiegelhalter et al. 2002).

We based our conclusions on the 95% Bayesian credibility intervals of Eq. 2. Each individual significance test was at the 5% level, and we did not adjust the tests to give an experiment-wide error rate of 5%. In evaluating the effect of herbicide on frequency we often

assessed whether or not the 95% credibility interval of the "herbicide β " overlapped 0. In several cases where the effect of herbicide depended on grazing, it was necessary to have separate "herbicide β 's" for each grazing treatment and compare these β 's to 0. Finally, model-selection procedures did not always support inclusion of "herbicide β 's", and in these cases it was logical to conclude herbicide had no effect.

Biomass data analysis

We used the following bivariate regression model to estimate herbicide effects on grass and *Euphorbia esula* biomass production:

$$\mathbf{P}_{ijklm} = \mathbf{M}_j + \mathbf{B}_k + \mathbf{H}_{lj} + \mathbf{G}_{mj} + \varepsilon_{ijklm}$$
(3)

where all symbols represent vectors of length two. One element of these vectors represents grasses whereas the other element represents E. esula. Transformed biomass production for plot *i*, year *j* is given by \mathbf{P}_{ij} , while other symbols describe year-specific means (M_i) , the replication k effect (\mathbf{B}_k), and year-specific herbicide (\mathbf{H}_{li}), and grazing (G_{mi}) effects. Model-selection procedures did not support the need for any additional interaction terms. To meet linear-regression assumptions, grass data were natural-log transformed and E. esula data were square-root transformed, but our results are presented in back-transformed units. The ε_{ijklm} were assumed to follow a multivariate normal distribution and a widely used noninformative prior distribution was assigned to the residual covariance matrix (\mathbf{R}) and the regression coefficients: $p(\mathbf{M}, \mathbf{B}, \mathbf{H}, \mathbf{G}, \mathbf{R} | \mathbf{X}) \propto |\mathbf{R}|^{-3/2}$ (Gelman et al. 2004). Again, we used MCMC to simulate the posterior distribution. We based our conclusions on credibility intervals for the marginal distributions for the herbicide coefficients (\mathbf{H}_i) .

RESULTS

Frequency data results

Except for *Euphorbia esula*, herbicide initially greatly depleted all exotic forbs and none of them recolonized appreciably by one year after application (data not shown). However, all but one exotic forb recolonized by four years after application, and by 16 years after application exotic-forb frequencies did not differ statistically between sprayed and not-sprayed plots (Fig. 1).

Similar to the exotic forbs, herbicide continued to suppress three natives as a group (i.e., *Rosa woodsii*, *Sphaeralcea coccinea*, and *Artemisia lucoviciana*) one year after application (data not shown), and like the exotics, these plants recovered by the study's end (see "sparse natives" in Fig. 1). Another native-forb group (*Androsace* spp.) was apparently unaffected by herbicide; it was similarly abundant in sprayed and notsprayed plots throughout the study. This was not surprising because even within a plant genus particular herbicides often kill some species while leaving others little harmed (Wang and Dekker 1995). Two native

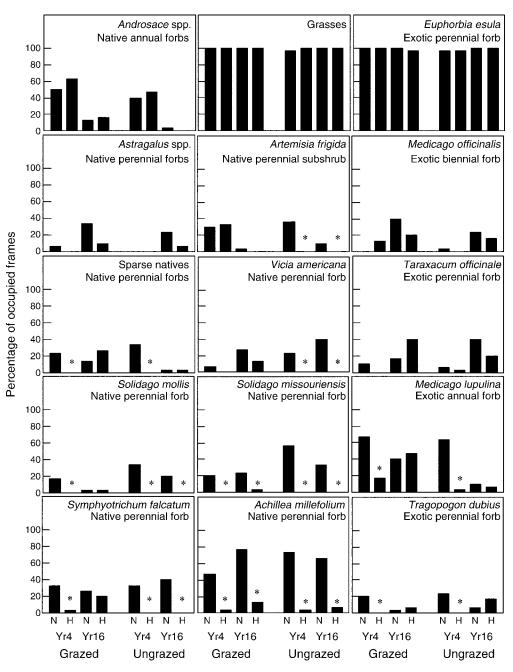


FIG. 1. Plant frequency data from study with herbicide (H = herbicide vs. N = no herbicide) and grazing (grazed vs. ungrazed) treatments. Data are from 4 and 16 years after herbicide application. A bar with an asterisk is significantly different from the bar immediately to the left ($P \le 0.05$), and we made only these pairwise comparisons. Significance tests were based on 95% Bayesian credibility intervals.

forbs that were initially greatly suppressed by herbicide never fully recovered from herbicide use regardless of grazing (*Solidago missouriensis* and *Achillea millefolium*) (Fig. 1). Finally, three native forbs (*Solidago mollis*, *Symphyotrichum falcatum*, *Vicia americana*) and a subshrub (*Artemisia frigida*) were significantly rarer in sprayed plots 16 years after spraying but only when grazing was excluded (Fig. 1).

Biomass data results

Herbicide reduced production of the dominant invasive species (*E. esula*) for several years (Fig. 2). Alternatively, herbicide increased grass production the year of application and most likely the following year (Fig. 2). Presumably, these grass increases resulted from reduced production and competition by dicot species (Figs. 1 and 2).

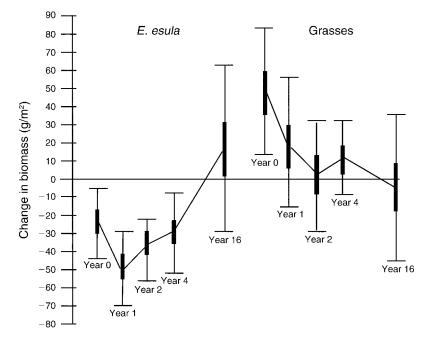


FIG. 2. Change in *Euphorbia esula* and grass biomass due to herbicide use one month (year 0) and 1, 2, 4, and 16 years after herbicide application. Lines connect posterior distribution modes, while "boxes" and "whiskers" denote 75% and 95% Bayesian credibility intervals, respectively.

Based on the posterior distribution of biomass model parameters, there is a 0.76 probability herbicide increased *E. esula* production during the 16th year after application (Fig. 1). If *E. esula* production did increase from herbicide use, a likely cause is reduced production and competition by native dicot species (Fig. 2).

DISCUSSION

Aside from a transient increase in grass forage production (Fig. 2), herbicide provided little benefit to the livestock producer or the ecosystem we studied. One of the primary objectives of spraying was to increase cattle forage by decreasing Euphorbia esula production, but paradoxically, two sources of evidence suggest that herbicide ultimately increased E. esula production. One such source of evidence is the final E. esula point estimate of Fig. 2, but measurement error caused considerable uncertainty in this estimate. The other source of evidence extends from the observation that spraying reduced native-forb abundances (Fig. 1). Other research has shown that grasses and forbs compete with the invasive species *E. esula* (Rinella and Sheley 2005), so reduced native-forb abundances should lead to increased E. esula production.

In addition to *E. esula*, all other exotic species also eventually recovered from spraying (Fig. 1). In contrast to the exotics, herbicide caused long-term suppression of several native forbs (Fig. 1).

The native-forb responses we witnessed contrast sharply with observations from a previous study. Like us, Rice et al. (1997) treated an invader (*Centaurea maculosa*) with picloram, but, unlike us, they detected little or no lasting effect on native forbs. Differences in herbicide toxicity may explain the difference between the studies. In our study, picloram initially greatly suppressed native forbs. Alternatively, in the Rice et al. (1997) study, the initial herbicidal response was quite mild; herbicide effects on native-forb cover and richness were subtle to nonexistent shortly after spraying. (Why herbicide toxicity would be so idiosyncratic is unclear to us, but herbicides could play a safer, more effective role in invasive-weed management if studies characterized conditions allowing natives to escape damage.) Taken together, the two studies show that native forbs are not always severely damaged by herbicides but when the forbs are damaged there can be long-lasting negative consequences. Aside from native forbs, our results are similar to those of Rice et al. (1997). In both studies, the weed ultimately recovered from herbicide damage and evidence was lacking for long-term increases in grass production due to herbicide use.

Our unsettling results appear all the more disconcerting in light of our experimental design. Four plots within a replicate were arranged two columns by two rows with zero between-plot spacing, so ample opportunity existed for propagule exchange between plots. Therefore, some native individuals occurring in sprayed plots may have immigrated as seeds from adjacent not-sprayed plots over the 16-year study period. Consequently, our sprayed plots were privy to external sources of native propagules that are not typically present following largescale spraying operations. Therefore, because of adjacent "seed-source islands" our study may underestimate deleterious effects of large-scale spraying on native-plant



PLATE 1. Cattle on leafy spurge-infested rangeland near Terry, Montana (USA). Photo credit: Richard Waterman.

communities. Yet, this argument might seem flawed because, like the natives, the exotics could also recolonize from not-sprayed plots. However, herbicide never made the dominant exotic species (*E. esula*) rare. *E. esula* occurred in over half the sprayed-plot sampling frames during every year of sampling. Therefore, instead of relying on immigrating propagules, *E. esula* likely repopulated from surviving propagules within the sprayed plots.

It is important to speculate on mechanisms driving our measured responses. Specifically, do our data reflect prolonged herbicidal effects from picloram in the soil or the plant community relaxing toward equilibrium in the absence of herbicide? If the herbicide remained active for our study's duration, then all species might still revert to their pre-herbicide abundances when the chemical finally does dissipate. Conversely, if the herbicide was inactive for much of the study, then our measured responses probably reflect long-term plant-community change. Several sources of information indicate the herbicide deactivated long before the study's end. First, Wauchope et al. (1992) reviewed the literature and reported the average picloram soil half-life to be 90 d, and the lowest picloram concentration ever shown to have a phytotoxic effect is 0.0000139 kg/ha (Environmental Protection Agency 1995). Based on these values, picloram would have reached nontoxic concentrations no longer than four years post-application. Second, when soil picloram levels were periodically measured in another Montana-grassland weed study, the herbicide reached nontoxic levels within two years of application (Rice et al. 1997). Furthermore, our plant data themselves provide very compelling evidence the herbicide dissipated early in the study. Firstly, there is evidence E. esula, a picloram-sensitive species, eventually became most abundant in herbicide-treated plots-a highly improbable outcome in the presence of toxic herbicide concentrations (Fig. 2). Secondly, several native forbs fully recovered with grazing but not without it. While grazing can alter forb abundances (Loeser et al. 2007), it should have little effect on herbicide-dissipation rates. Finally, five forbs that were absent from herbicidetreated plots the year following application were present three years later, suggesting that the herbicide dissipated within three years of application.

If prolonged toxilogical effects do not explain our main findings, what does? One finding was that herbicide caused several natives to become rare (or perhaps absent), but only if grazing was excluded. In addition to increasing light availability by removing standing vegetation, livestock also disturb soil, which can provide idyllic microsites for seedling establishment (Oesterheld and Sala 1990, Hayes and Holl 2003). In addition to providing microsites for seedlings, grazing animals probably increased seed densities through hoof and fur transport of seeds from not-sprayed plots and elsewhere (Couvreur et al. 2004). Thus it is not too surprising that several natives recovered from herbicide with but not without grazing. What is somewhat surprising, however, is that these same native forbs did not decline without herbicide when grazing was excluded; several grassland studies show forbs declining after cattle exclusion (e.g., Towne et al. 2005, Vulliamy et al. 2006).

Herbicide caused two natives (Solidago missouriensis in grazed plots and Achillea millefolium) to become rarer for our study's duration. This rarity could denote herbicide's hastening of a preexisting process, namely, the gradual replacement of natives by exotics at the site. A problem with this depiction, however, is that these natives did not decline in not-sprayed plots over a protracted period (i.e., 16 years; Fig. 1). This suggests that, barring herbicide use, A. millefolium and S. missouriensis were capable of coexisting indefinitely with the exotics. But even though the natives were not necessarily destined for extinction, neither were they able to recover original population sizes after herbicide use (Fig. 1). Several plausible mechanisms could explain the prolonged rarity of these natives. Perhaps the natives act as fugitives in the system; i.e., they coexist by rapidly colonizing gaps occurring when the dominant species (E. esula and grasses) die. If so, the natives likely became recruitment limited due to the herbicide's presumably large negative effect on seed production. As seed production becomes lower, so does the probability of seeds being available to colonize gaps created by grass and E. esula mortality. Theoretically, recruitment limitation can have enduring consequences; when simulated species are perturbed in competitor-fugitive models population trajectories can vacillate for hundreds of simulated years before settling to equilibrium (Tilman 1994, Hurtt and Pacala 1995).

Regardless of the responsible mechanism(s), herbicide use made *A. millefolium* and *S. missouriensis* rare for a long time, and these natives will remain highly susceptible to demographic stochasticity and disturbance as long as they are rare. One disturbance that could eventually drive the natives locally extinct is a second herbicide application; researchers sometimes encourage multiple applications for invasive-weed control (Lym 2000, Shinn and Thill 2003).

Controlling invasive weeds with herbicides is not categorically ill advised. Many natural areas are highly degraded with few or no remaining native dicot species. In these areas, dicot herbicides sometimes increase native and nonnative grass forage production (Lym and Messersmith 1994, Sheley et al. 2004). Furthermore, herbicides are sometimes used to suppress invaders so that native species can be reintroduced through seeding or other means (Tyser et al. 1998, Sheley et al. 2006). Perhaps more importantly, herbicides can be effective for eradicating small weed patches or interrupting the spread of large patches along advancing invasion fronts.

Conversely, our results suggest "broadcasting" herbicides over large areas containing herbicide-sensitive native populations is sometimes ill advised. According to our study, it cannot safely be assumed that large-scale spraying of nonarable lands will always provide longterm benefits to livestock producers or that native species will always recover from herbicide damage. Our study presents a cautionary tale about invasive-species management: the treatment can be worse than the disease. This finding could turn out to be relevant in many invasive-species management scenarios, not just for herbicides and not just for grasslands. Regardless of the ecosystem, it is generally the latter stages of invasion that provoke aggressive and potentially damaging management efforts. Unfortunately, the sheer abundance of invaders at these latter stages generally ensures plenty of individuals will escape control, and these escaping individuals tend to quickly reinvade (e.g., Emery and Gross 2005). Moreover, native populations are often much smaller than co-occurring invader populations, and our study shows these smaller populations can fail to recover from damage imposed by invasive-species management. Therefore, when invasivespecies management has the potential to damage native species, not managing may be preferable in some situations.

ACKNOWLEDGMENTS

We thank Tom Elliot, the land owner, for allowing this longterm study to be conducted on the N-Bar Ranch. We also thank Patrick Plantenberg, Bob Rennick, Celestine Lacey, Tim Chicoine, Bill Dyer, and John Lindquist for their many hours of field work.

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