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GRASSLAND INVADER RESPONSES TO REALISTIC CHANGES IN NATIVE SPECIES RICHNESS

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Abstract. The importance of species richness for repelling exotic plant invasions varies from ecosystem to ecosystem. Thus, in order to prioritize conservation objectives, it is critical to identify those ecosystems where decreasing richness will most greatly magnify invasion risks. Our goal was to determine if invasion risks greatly increase in response to common reductions in grassland species richness. We imposed treatments that mimic management-induced reductions in grassland species richness (i.e., removal of shallow- and/or deep-rooted forbs and/or grasses and/or cryptogam layers). Then we introduced and monitored the performance of a notorious invasive species (i.e., *Centaurea maculosa*). We found that, on a per-gram-of-biomass basis, each resident plant group similarly suppressed invader growth. Hence, with respect to preventing *C. maculosa* invasions, maintaining overall productivity is probably more important than maintaining the productivity of particular plant groups or species. But at the sites we studied, all plant groups may be needed to maintain overall productivity because removing forbs decreased overall productivity in two of three years. Alternatively, removing forbs increased productivity in another year, and this led us to posit that removing forbs may inflate the temporal productivity variance as opposed to greatly affecting time-averaged productivity. In either case, overall productivity responses to single plant group removals were inconsistent and fairly modest, and only when all plant groups were removed did *C. maculosa* growth increase substantially over a no-removal treatment. As such, it seems that intense disturbances (e.g., prolonged drought, overgrazing) that deplete multiple plant groups may often be a prerequisite for *C. maculosa* invasion.

Key words: Bayesian; biodiversity; Centaurea maculosa; *forbs; grasses; invasibility; invasion resistance; local extinction; spotted knapweed.*

INTRODUCTION

Human activity is reducing biodiversity throughout the globe (Pimme et al. 1995, Vitousek et al. 1997). There is concern that species-deprived ecosystems will have greater resource availabilities and exotic species could use the surplus resources to invade (Davis et al. 2000, Lyons and Schwartz 2001). Consequently, diversity–invasibility relationships have become intensely studied.

To date, diversity–invasibility studies have focused almost exclusively on testing and refining theory (e.g., Tilman 1997, Kennedy et al. 2002, Milbau et al. 2003, Fargione and Tilman 2005), while invader responses to real-world, human-induced, species losses have gone largely unstudied. The theory-oriented studies have and will continue to provide crucial insight. However, the studies have been somewhat artificial with respect to real-world extinction events. Specifically, random extinctions have been the focus (e.g., Fargione and Tilman 2005, Milbau et al. 2005), whereas real-world extinctions are nonrandom because particular stressors affect some plant groups differently than others (Huston et al. 1998, Duncan and Young 2000). This and other abstractions will matter less as the data coalesce into general invasibility theory; truly general theory will predict invader responses to random and nonrandom extinctions alike. But diversity-invasibility relationships have proven highly idiosyncratic (e.g., Prieur-Richard et al. 2000 vs. Eriksson et al. 2006) and the experimental data have proven difficult to interpret (Huston 1997, Wardle 2001). Consequently, general theory has been slow to develop. Moreover, particular species or functional groups can be indispensable drivers of ecosystem processes (such as invasion resistance) in some environments while being much less important elsewhere (Wardle and Zackrisson 2005). And this complicates efforts to predict if, when, and where local species losses will magnify invasion risks.

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Given the uncertainty surrounding invader responses to local extinctions, it seems to us some extinction scenarios could profit from direct empirical investigations. The first step in these investigations would entail asking "which groups of species are being lost?" Then studies could be designed to characterize invader responses to these losses. This paper illustrates such an approach. We feel this pragmatic approach may become critical for setting conservation priorities, especially in habitats where invasions are clearly eminent and local species losses are commonplace. One such habitat is the focus of our study; i.e., the Idaho fescue/bluebunch wheatgrass (*Festuca idahoensis*/*Agropyron spicatum* [*Pseudoroegneria spicata* (Pursh) A. Löve]) habitat type of the western United States (Mueggler and Stewart 1980). This conservation-critical, intermountain habitat type is widely distributed throughout the west, and many former bunchgrass sites are already dominated by Eurasian plants, such as sulfur cinquefoil (*Potentilla recta* L.) and spotted knapweed (*Centaurea maculosa* Lam.) (Sheley and Petroff 1999).

In addition to being threatened by invasion, management practices in western bunchgrass habitats sometimes deplete or remove three groups of species; i.e., grasses, forbs, and cryptogamous plants. Overgrazing by cattle is the principle cause of grass depletions (Mack and Thompson 1982, O'Connor 1991), while native forbs are sometimes herbicide treated to increase grass forage production or curb livestock poisonings by species like tall larkspur (*Delphinium glaucum* S. Wars.) (Ralphs et al. 1990). In addition to being purposely targeted, native forbs also serve as collateral targets when invasive weeds or sagebrushes (*Artemesia* spp.) and other shrubs are sprayed to increase grass forage production (e.g., McDaniel et al. 2005); i.e., invasive weed and shrub herbicides kill native forbs. Finally, cryptogam layers comprised of spikemosses and other non-vascular plants are a prevalent feature of western bunchgrass habitats. Livestock trampling can destroy these crusts (Warren and Eldridge 2003), and the belief that soil crusts lower forage production has generated interest in mechanically removing them (Kulshreshtha et al. 2002).

We imposed plant group removal treatments (removal of grasses, forbs, or cryptogam layers) that mimic plant group losses/depletions common to bunchgrass habitats. Then we introduced seeds of a notoriously invasive species (*Centaurea maculosa* Lam.). We collected data on invader growth and resident community biomass and used these data to answer questions about roles of resident plant groups in preventing *C. maculosa* invasions. In another paper, the questions pertained to *C. maculosa* seedling establishment (Pokorny et al. 2005), while the current paper focuses on post-establishment growth.

One of our objectives was to assess effects on resident biomass production of removing resident plant groups. Our other objective was to estimate per-gram-of-biomass competitive effects of resident plant groups on *C. maculosa* growth. Several studies have reported that each neighbor species affected the target species similarly on a per-gram basis (Goldberg 1987, Miller and Werner 1987, Peart 1989). If resident plant groups (neighbors) affect *C. maculosa* (target) similarly on a per-gram basis, and if the per-gram effects of multiple plant groups do not interact synergistically, then this would suggest overall productivity is what matters most for repelling invasions. In this case, high richness will discourage *C. maculosa* invasion only when it leads to increased productivity. In contrast with this view is a recent study where invader growth was negatively related to species richness even after productivity patterns were controlled for (Fargione and Tilman 2005), and this study suggests increased productivity is but one of multiple mechanisms by which diversity can discourage invasion. From the standpoint of our investigation, if per-gram effects of resident plant groups are similar and do not interact, we will conclude overall resident vegetation productivity is a good indicator of invasibility. In this case, we will conclude that plant group removals that reduce productivity will appreciably magnify invasion risks. On the other hand, if some plant groups turn out to be atypically strong per-gram competitors, then biomass production alone may be a poor indicator of invasion risks. In this case, it may be important to prioritize conserving the strong per-gram competitors (sensu Power et al. 1996), even if their absence does not reduce overall productivity.

Methods

Sites

An earlier study using the same field plots evaluated *C. maculosa* establishment (Pokorny et al. 2005), while our study investigated post-establishment growth. Our research sites and experimental design are described in detail (Pokorny et al. 2005), so we reiterate just those aspects of relevance to the current study. The research was conducted on two sites in southeastern Montana, USA. The sites were slightly less the 1.0 km apart but differed somewhat in plant composition and soil chemistry. Prior to our study, *C. maculosa* was quite rare at both sites (<1% cover).

Experimental design

Plant group removal treatments were arranged in a randomized complete block design with four replications at each site. A factorial arrangement of treatments (7 removal treatments × 2 *C. maculosa* treatments) was applied to 2 × 2 m plots. The removal treatments were designed to simulate local extinctions/depletions common to bunchgrass habitats. We removed (1) nothing; (2) cryptogam layers (seven species); (3) shallow-rooted forbs (17 species); (4) deep-rooted forbs (22 species); (5) all forbs (39 species); (6) all grasses (14 species); and (7) all plants (60 species). The invader treatments were *C. maculosa* (1) not seeded; and (2) seeded. Separate treatments for deep- and shallow-rooted forbs were included because rooting depth partially determines forb responses to drought (Weaver et al. 1935, Skinner et al. 2004). Forb species with roots never or only rarely extended below 15 cm into the soil were assigned to the shallow-rooted category. Rooting depths were determined by excavating plants adjacent to the research sites.

Except for cryptogam layers, which were removed by hand pulling, plants were removed with a glyphosate (N-[phosphonomethyl] glycine) solution, which was brushed onto plants early in the 2000 growing season. *C. maculosa* seeds (8000 per plot) were sown after plant growth ceased in fall 2000. This was the only seed input; seed heads were removed from plants prior to seed rain to prevent *C. maculosa* from spreading from the study areas.

Sampling

Vegetation data were collected in 2001, 2003, and 2004. To account for possible between-species differences in growth and senescence times (Pokorny et al. 2004), biomass samples were gathered during three sampling periods within each year. Plots were divided into three equally sized subplots and early June, July, and August sampling periods were randomly assigned to the subplots. During each sampling period, vegetation (except cryptogam layers) was clipped at soil level from three 20 × 50 cm frames placed at random within subplots. Plant material was separated into *C. maculosa*, grass, shallow-rooted forb, and deep-rooted forb components. Components were dried (40°C, 160 h) and weighed.

Analysis

In estimating per-gram competitive effects of resident plant groups on *C. maculosa* growth, our response variable was *C. maculosa* mass per plant. Average masses per plant for each plot were calculated by averaging masses over the three sampling periods within each year. We based our analysis on 2003 and 2004 plant mass data; 2001 masses were not analyzed because all *C. maculosa* plants were still very small at the end of their first growing season (<1.0 g per plant; Pokorny et al. 2005). (An exception to this was the completely devegetated plots, where average individual masses exceeded 3.0 g per plant in some plots.) We restricted our plant mass analysis to plots where nine or more *C. maculosa* individuals established. This provided more reliable plant mass data by ensuring the expected number of weighed individuals exceeded 2.0 per plot. The numbers of plots per treatment with nine or more plants were: 0, remove nothing; 0, remove cryptogam layers; 3, remove shallow-rooted forbs; 5, remove deep-rooted forbs; 6, remove grasses; 8, remove all forbs; and 8, remove everything. In modeling individual *C. maculosa* plant masses, we evaluated explanatory variables describing sites, replications, years, 2001 *C. maculosa* mass per plant, biomass of shallow-rooted forbs, deep-rooted forbs, and grasses, and interaction terms. Terms describing cryptogam layer effects were omitted because *C. maculosa* establishment was extremely low when only cryptogam layers were removed (Pokorny et al. 2005).

In evaluating effects of plant removals on resident community biomass production, we used data from 2001, 2003, and 2004. Per-plot biomasses were estimated as resident plant masses (cryptogamous plants excluded) summed over the three sampling periods within a year. Plots were included in the community biomass analysis if *C. maculosa* was not sown, or if it made up <2% of the biomass. Prior to including plots where *C. maculosa* was sown but did not appreciably establish, we verified (via scatterplots) that resident biomass patterns did not explain the establishment failures. In modeling resident community biomass, we evaluated predictor variables representing sites, replications, years, removal treatments, and interactions.

C. maculosa plant mass and community biomass datasets were analyzed with univariate and multivariate normal linear regression models. We used a model selection criterion (i.e., Bayes factor) to determine whether univariate or multivariate models best described our datasets (Kass and Raftery 1995). In addition to aiding decisions regarding univariate and multivariate models, Bayes factors also helped identify predictor variables lacking explanatory power. This enabled us to eliminate unnecessary variables and develop parsimonious models.

Community biomass data were best described by a multivariate model. With this model, we considered each year's data to be a separate response; i.e., each year's response data constituted one dimension of a multivariate response. In addition, the multivariate model had separate (but potentially correlated) regression coefficients for each combination of predictor variable and year. The model can be expressed as

$$C_{ijkm} = \mu_i + L_{ij} + \beta_{ik} + \varepsilon_{ijkm} \qquad (1)$$

where C_{ijkm} is non-cryptogam community biomass for year i realized at site j for treatment k and plot m, μ_i is the overall mean for year i, L_{ij} is the site j effect in year i, β_{ik} is the removal treatment k effect in year i, and ε_{ijkm} is random error.

The multivariate model included a residual (co)variance matrix describing variation within years and covariation among years. It was assumed that

$$\boldsymbol{\varepsilon} = (\boldsymbol{\varepsilon}'_{2001}, \boldsymbol{\varepsilon}'_{2003}, \boldsymbol{\varepsilon}'_{2004})' \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R}) \qquad (2)$$

where $\boldsymbol{\varepsilon}$ terms within brackets represent random error vectors subscripted by the years of data collection, $\mathbf{R}$ is a 3 × 3 residual (co)variance matrix, and $\mathbf{I}$ is the identity matrix.

A univariate model was the best descriptor of spotted knapweed plant mass data:

$$\ln(K_{ij}) = \mu + T_i + L_j + \beta_s X_{1ij} + \beta_d X_{2ij} + \beta_g X_{3ij} + \varepsilon_{ij} \quad (3)$$

where μ is mean *C. maculosa* plant mass over the entire study, T_i is the year *i* effect, L_j is the site *j* effect and β_s, β_d, and β_g are biomass effects of shallow- and deep-rooted forbs and grasses, respectively. There is no cryptogam layer term because cryptogam-removal plots had low *C. maculosa* establishment and were therefore excluded from our analysis. The natural logarithm transformation helped validate the normality assumption. Unlike the multivariate model, Eq. 3 does not contain separate regression coefficients for each year of data collection. Thus the *T* terms are included to help account for potential serial correlations among annually repeated measurements. Also, we speculated that the level of residual variation might differ among years, so we estimated separate residual variances for each year of data collection.

We used nonhierarchical Bayesian methods to fit our models, so assigning prior distributions to the regression coefficients, variances, and covariances was a necessary step in our analysis. In all cases, commonly used noninformative priors were used (Gelman et al. 2004). In order to investigate the effect of prior distributions on the final results, a sensitivity analysis was conducted where several different non-informative priors were assumed for the model parameters. The sensitivity analysis showed that the choice of noninformative prior distributions affected our results only slightly. The non-informative prior distributions we used provided parameter estimates similar to those that would be obtained with classical statistical procedures. However, there is a difference between the interpretations of classical and Bayesian parameter estimates. In contrast to the complicated interpretation of a classical 95% confidence interval, the 95% Bayesian credibility intervals we present are interpreted simply as having a 95% chance of containing the true parameter value.

All inferences were based on the joint posterior distributions of regression coefficients and dispersion parameters. If the 95% Bayesian credibility intervals on compared parameters did not overlap, we concluded that the parameters differed. Markov Chain Monte Carlo integration (i.e., Gibbs sampler) was used to simulate the posterior distributions. Given our assumptions about the data distributions (i.e., that they were normal) and the prior distributions, the conditional distributions needed for carrying out the integrations were in close form. The position parameters (regression coefficients) were normal, while the dispersion parameters (residual variances and **R**) were inverse chi-square in the univariate case and inverse Wishart in the multivariate case (Gelman et al. 2004). To simulate posterior distributions, sample statistics were assigned as starting values and then the parameter values were repeatedly updated by drawing sequentially from the conditional posterior distributions of regression coefficients and dispersion parameters. A Markov chain consisting of 200 000 draws for each parameter was constructed and the first 100 000 draws were discarded as burn-in. To ensure convergence was achieved, we constructed a second chain and compared the resulting parameter estimates to those acquired from the first chain. All computations were performed using a FORTRAN 6.6.a (Compaq Computer Corporation, Houston, Texas, USA) program developed by the first author.

RESULTS

Effect of plant removals on resident community biomass production

We attempted to guard against between-plant group differences in growth and senescence times by sampling biomass at three time points within growing seasons. Proportionally, biomasses of shallow- and deep-rooted forbs and grasses turned out to be very consistent across the sampling periods (data not shown), so multiple samplings were probably unnecessary.

The β coefficients of Eq. 1 describe effects of plant group removals on community biomass. More specifically, these coefficients represent mean biomasses over all plots receiving the same treatment. Fig. 1 summarizes these means and the statistical differences between them. In 2001, plots with all forbs removed yielded lowest. Plots with no forbs produced more biomass than the other plots in 2003. In 2004, plots with only deep-rooted forbs removed yielded lower than no-removal plots. Removal effects on biomass production were consistent across site, as is indicated by the lack of interaction terms in Eq. 1.

Effect of community biomass production on C. maculosa *growth*

Fig. 2 shows mean *C. maculosa* densities and plant masses over time by treatment. The no-removal and cryptogam-removal treatments are omitted from Fig. 2 due to poor establishment; only one individual was present in a no-removal plot at the end of the study, while cryptogam-removal plots contained a total of six individuals.

Terms describing site interactions are absent from Eq. 3 because these terms did not improve model performance. This suggests competitive effects of native plant groups on *C. maculosa* growth did not vary between the study sites. Terms describing interactive effects between plant groups are also omitted. This implies that the effect of a given plant group on *C. maculosa* growth was independent of the abundances of the other plant groups. The β coefficients of Eq. 3 have intuitive interpretations. Specifically, these coefficients represent percent changes in *C. maculosa* plant masses resulting from 1.0 g/m^2 changes in resident plant group biomass production. The 95% Bayesian credibility intervals on β_s, β_d, and β_g greatly overlap, indicating shallow- and deep-rooted forbs and grasses suppress *C. maculosa* growth similarly on a per-gram basis (Fig. 3).

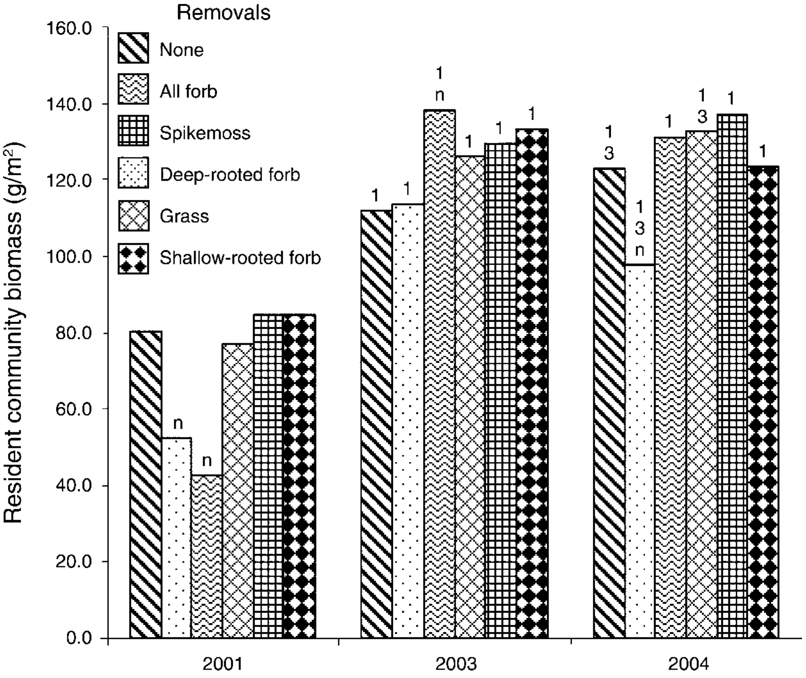

FIG. 1. Mean biomass production in plots with resident plant groups removed. Numbers above bars signify statistically significant differences ($P < 0.05$) between years (e.g., a 2004 bar topped with 1 and 3 is different than 2001 and 2003). Within a given year, bars topped with n are different than bars with no removal.

DISCUSSION

Effects of resident plant groups on C. maculosa *seedling establishment*

An earlier study of our same field plots evaluated *C. maculosa* seedling responses to grass, forb, and cryptogam layer removals (Pokorny et al. 2005). It was found that seedling establishment increased when forbs were absent (Fig. 2), which suggests forbs are particularly important for preventing *C. maculosa* invasion. Removing forbs reduced overall productivity during the period when *C. maculosa* seedlings were establishing (2001 data, Fig. 1), which suggests increased productivity (i.e., resource use) as the mechanism by which forbs discouraged establishment. Growing season precipitation during 2001 provides further evidence that forbs are important for maintaining productivity and preventing invader establishment. Proportionally, forbs sometimes produce more biomass in dry years (Briggs and Knapp 1995), and the 2001 growing season was quite dry (540 mm from 1 April through 31 July) in comparison to the other years of our study (~200 mm in 2003 and 2004). Thus, productivity may have been lowest in forb-removal plots in 2001 because 2001 was dry. However, we hasten to add that the pattern of lower productivity and increased *C. maculosa* establishment in the absence of forbs has a second interpretation. Specifically, this pattern could have been caused by large plant community gaps; i.e., gaps caused by forb removals. More specifically, *C. maculosa* sowing may have occurred before resident plants fully equilibrated to forb removals. And if the plants lacked time to "fill in" after forb removals, then the increased *C. maculosa* establishment we witnessed could be an experimental artifact. So our data are inconclusive about the role of forbs in preventing *C. maculosa* establishment. On the other hand, our data are conclusive in showing that intact bunchgrass communities can be highly resistant to invader establishment (Fig. 2), and this suggests past invasions may be a response to management or prolonged drought that depleted one or more plant groups.

Effects of resident plant groups on C. maculosa *growth*

While our data are not ideally suited for studying *C. maculosa* establishment, they are well suited for studying post-establishment growth. And the post-establishment growth phase is critical to *C. maculosa* population viability; a demographic study has highlighted the importance of young plant (i.e., rosette) growth and survival to *C. maculosa* invasion dynamics (Jacobs and Sheley 1998). In our study, shallow- and deep-rooted forbs and grasses affected *C. maculosa* growth similarly on a per-gram basis, and the per-gram effect of any one group was unaffected by the biomass production of other groups; i.e., there were no significant interactions. This implies that the numbers of species within the forb and grass groups were large enough that diversity effects saturated. Ours is not the first study to suggest a saturating relationship between diversity and invader performances (e.g., Naeem et al. 2000, Milbau et al.

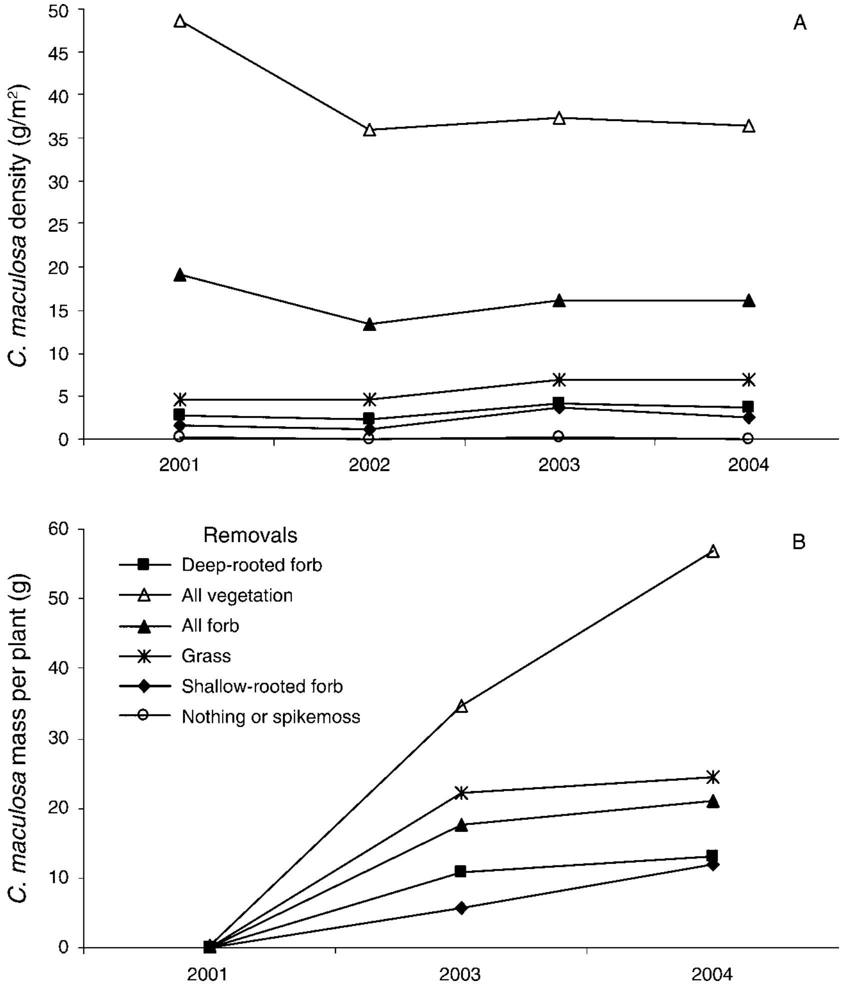

FIG. 2. (A) Mean *Centaurea maculosa* densities and (B) individual plant masses resulting from plant group removal treatments during the period 2001–2004.

2005). And it is not particularly surprising that the saturation level is sometimes reached in plant assemblages comprised exclusively of forbs or grasses. Forb and grass groupings can be poor predictors of functional attributes (Wright et al. 2006); i.e., at a given species richness level, groups comprised of forbs *or* grasses can be as functionally diverse as groups comprised of forbs *and* grasses.

Effects of resident plant group removals on productivity and invasion risks

Given that our study's per-gram competitive effects did not differ appreciably among plant groups, we conclude that maintaining the number of grams of biomass produced (i.e., productivity) is what matters most for repelling *C. maculosa* invasions. And it is overall productivity that matters, not the productivity of particular plant groups. However, all plant groups may be needed to maintain overall productivity. For instance, in 2001, plots with deep-rooted forbs removed yielded lower than plots containing all plant groups (Fig. 1). This lower yield could reflect sampling effects (Huston 1997, Wardle 2001) or niche partitioning between forbs and grasses (Tilman et al. 2001, Hector et al. 2002), or as mentioned above, it could simply be an experimental artifact resulting from plants lacking sufficient time to equilibrate to 2000 plant removals. The 2004 data provide stronger evidence that deep-rooted forbs are important contributors to overall productivity; plots with deep-rooted forbs removed yielded lower than intact plots in this year (Fig. 1). But it is peculiar that plots with both deep- and shallow-rooted forbs removed did not under-yield intact plots in 2004. That productivity was reduced by removing a portion of the forbs but not all the forbs was unexpected. We refrain from offering an explanation for this result because several plausible explanations exist, and our data do not convincingly refute or corroborate any of them.

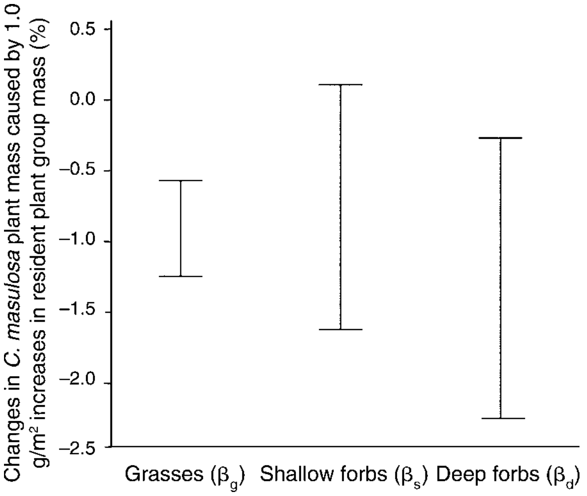

FIG. 3. The 95% Bayesian credibility intervals on competitive impact parameters (β_s, β_d, and β_g are biomass effects of shallow- and deep-rooted forbs and grasses, respectively). Parameters describe *Centaurea maculosa* plant mass responses to competition by grasses and shallow- and deep-rooted forbs (see Eq. 3 for model).

In contrast to 2001 and 2004, removing forbs increased productivity in 2003, and this certainly tempers our conclusion that forbs are critical for maintaining productivity (Fig. 1). In fact, this finding opens up the possibility that, averaged over many years, the grassland we studied is more productive without forbs. To us, this seems unlikely, in part because it goes against an existing body of theory and empiricism (Naeem et al. 1996, Tilman et al. 2001, Hector et al. 2002). Instead, it seems more likely that removing forbs inflated the temporal productivity variance (i.e., productivity variance calculated over many years) as opposed to inflating the temporal productivity mean (i.e., time-averaged productivity). The idea that removing plant groups increases productivity variation enjoys strong empirical support (Tilman et al. 2006).

And how might *C. maculosa* respond to the increased productivity variation that results from removing forbs? Inflated productivity variation implies an increased incidence and magnitude of low-productivity years, with the low-productivity years being a consequence of fewer resource users (i.e., forbs), not fewer resources. At a given resource supply rate, fewer resource users will lead to increased resource availabilities, and it is widely held that increased resource availabilities will encourage invasions (Davis et al. 2000, Davis and Pelsor 2001). Thus, invasion risks probably increase after forbs are removed because resource availabilities become uncharacteristically high, particularly in years where grass growth does not compensate for the absence of forbs.

Yet, removing forbs only mildly impacted productivity in our study (Fig. 1), and at a glance, this seems to imply forbs play but a minor role in maintaining productivity and resisting invasions at the sites we studied. However, it may be that forbs are particularly important in poor grass years, and our sample of years did not include excessively poor grass years. The notion that some years are poor for grasses but good for forbs surpasses mere conjecture. For instance, if overstocking of cattle in a given year results in overgrazing of grasses, then grass production may be reduced but forb production might be unaffected (Pavlů et al. 2006), or forbs may even increase. Livestock were excluded from our study area, so our sample of years purposely excluded intense grazing years. And livestock grazing is not the only disturbance that differentially affects forbs and grasses; others include grasshopper outbreaks (Burleson and Hewitt 1982, Hewitt and Onsager 1983), and droughts (Briggs and Knapp 1995). Moreover, deeply rooted forbs can be particularly important contributors to overall biomass production and resource use in drought years (Weaver et al. 1935, Skinner et al. 2004). In summary, our study was too short and too limited in scope to characterize the role of forbs in "severe" years (i.e., years with intense grazing, drought or other disturbances), and the severe years may be when forbs are most important to overall productivity and invasion resistance.

There is much concern that local extinctions may promote exotic species invasions. Yet invader responses to realistic, nonrandom extinctions remain largely unstudied. Our investigation centered on species losses that are quite common within the system we studied. We feel this study yielded information of value to grassland managers struggling to prevent exotic weed invasions.

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LITERATURE CITED

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. American Journal of Botany 82:1024–1030.

Burleson, W. H., and G. B. Hewitt. 1982. Response of needle-and-thread and western wheatgrass to defoliation by grasshoppers. Journal of Range Management 35:223–226.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421–428.

Duncan, R. P., and J. R. Young. 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. Ecology 81:3048–3061.

Eriksson, O., S. Wikstrom, A. Eriksson, and R. Lindborg. 2006. Species-rich Scandinavian grasslands are inherently open to invasion. Biological Invasions 8:355–363.

Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters 8:604–611.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211–1223.

Hector, A., E. Bazeley-White, M. Loreau, S. Otway, and B. Schmid. 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. Ecology Letters 5:502–511.

Hewitt, G. B., and J. A. Onsager. 1983. Control of grasshoppers on rangeland in the United States: a perspective. Journal of Range Management 36:202–207.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460.

Huston, M. A., et al. 1998. No consistent effect of plant diversity on productivity. Science 289:1225a.

Jacobs, J. S., and R. L. Sheley. 1998. Observation: life history of spotted knapweed. Journal of Range Management 51:665–673.

Kass, R. E., and A. E. Raftery. 1995. Bayes factors. Journal of the American Statistical Association 90:773–795.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638.

Kulshreshtha, S. N., J. T. Romo, and H. Peng. 2002. Economic analysis of mechanically disturbing rangeland to reduce clubmoss in Saskatchewan. Canadian Journal of Plant Science 82:739–746.

Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function: invasion resistance. Ecology Letters 4:358–365.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119: 757–773.

McDaniel, K. C., L. A. Torell, and C. G. Ochoa. 2005. Economics and optimal frequency of Wyoming big sagebrush control with tebuthiuron. Rangeland Ecology and Management 58:77–84.

Milbau, A., I. Nijs, F. De Raedemaecker, D. Reheul, and B. De Cauwer. 2005. Invasion in grassland gaps: the role of neighborhood richness, light availability and species complementarity during two successive years. Functional Ecology 19:27–37.

Milbau, A., I. Nijs, L. Van Peer, D. Reheul, and B. De Cauwer. 2003. Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. New Phytologist 159:657–667.

Miller, T. E., and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. Ecology 68:1201–1210.

Mueggler, W. F., and W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. Intermountain Forest and Range Experimental Station, Ogden, Utah, USA.

Naeem, S., K. Hakenson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. Oikos 76:259–264.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. A. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

O'Connor, T. G. 1991. Local extinctions in perennial grasslands: a life-history approach. American Naturalist 137:753–773.

Pavlů, V., M. Hejcman, L. Pavlů, J. Gaisler, P. Hejcmanová-Nežerkova, and L. Meneses. 2006. Changes in plant densities in a mesic species-rich grassland after imposing different grazing management treatments. Grass and Forage Science 61:42–51.

Peart, D. R. 1989. Species interactions in a successional grassland. II. Colonization of vegetated sites. Journal of Ecology 77:252–266.

Pimme, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science 269:347–350.

Pokorny, M. L., R. L. Sheley, T. J. Svejcar, and R. E. Engel. 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. Western North American Naturalist 64:219–230.

Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. Restoration Ecology 13:448–459.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609–620.

Prieur-Richard, A.-H., S. Lavorel, K. Grigulis, and A. Dos Santos. 2000. Plant community diversity and invasibility by exotics: invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. Ecology Letters 3:412–422.

Ralphs, M. H., D. L. Turner, L. V. Mickelsen, J. O. Evans, and S. A. Dewey. 1990. Herbicides for control of tall larkspur (*Delphinium-Barbeyi*). Weed Science 38:573–577.

Sheley, R. L., and J. K. Petroff. 1999. Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis, Oregon, USA.

Skinner, R. H., D. L. Gustine, and M. A. Sanderson. 2004. Growth, water relations, and nutritive value of pasture species mixtures under moisture stress. Crop Science 44: 1361–1369.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92.

Tilman, D., P. B. Reich, K. Johannes, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science 294:843–845.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science 277:494–499.

Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? Oikos 95: 161–170.

Wardle, D. A., and O. Zackrisson. 2005. Effects of species and functional group loss on island ecosystem properties. Nature 435:806–810.

Warren, S. D., and D. J. Eldridge. 2003. Biological soil crusts and livestock in arid ecosystems: are they compatible? Pages 401–415 *in* J. Belnap and O. L. Lange, editors. Biological soil crusts: structure, function, and management. Springer-Verlag, Berlin, Germany.

Weaver, J. E., L. A. Stoddart, and W. M. Noll. 1935. Response of the prairie to the Great Drought of 1934. Ecology 16:612–629.

Wright, S. D., S. Naeem, A. Hector, C. Lehman, P. B. Reich, B. Schmid, and D. Tilman. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. Ecology Letters 9:111–120.