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ORIGINAL PAPER

# Native species richness buffers invader impact in undisturbed but not disturbed grassland assemblages

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**Abstract** Many systems are prone to both exotic plant invasion and frequent natural disturbances. Native species richness can buffer the effects of invasion or disturbance when imposed in isolation, but it is largely unknown whether richness provides substantial resistance against invader impact in the face of disturbance. We experimentally examined how disturbance (drought/burning) influenced the impact of three exotic invaders (*Centaurea stoebe*, *Linaria dalmatica*, or *Potentilla recta*) on native abundance across a gradient of species richness, using previously constructed grassland assemblages. We found that invaders had higher cover in experimentally disturbed plots than in undisturbed plots across all levels of native species richness. Although exotic species varied in cover, all three invaders had significant impacts on native cover in disturbed plots. Regardless of disturbance, however, invader cover diminished with increasing richness. Invader impacts on native cover also diminished at higher richness levels, but only in undisturbed plots. In disturbed plots, invaders strongly impacted native cover across all richness levels, as disturbance favoured invaders over native species. By examining these ecological processes concurrently, we found that disturbance exacerbated invader impacts on native abundance. Although diversity provided a buffering effect against invader impact without disturbance, the combination of invasion and disturbance markedly depressed native abundance, even in high richness assemblages.

**Keywords** Diversity · Drought · Exotic plants · Fire · Invasion

## Introduction

Many theoretical and experimental studies have demonstrated that diversity plays a key role in determining community response to external pressures (Hooper et al. 2005; Ives and Carpenter 2007). As natural systems face an increasing combination of anthropogenic pressures, much research has focused on understanding the effects of extrinsic factors, such as invasion and disturbance, on natural communities. Although many studies have addressed the relationship between diversity and invasion (see review in Levine and D'Antonio 1999), disturbance and invasion (see review in Hobbs and Huenneke 1992), or

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diversity and disturbance (see review in Hooper et al. 2005), few have examined how the interactions among all three factors impact native abundance within communities.

The level of diversity can affect community response to invasion, although other factors may determine whether invasion increases or decreases with diversity. Invasion can be promoted by declines in local native species richness due to an increase in resource availability (Tilman 1997; Naeem et al. 2000; Dukes 2002; Fargione and Tilman 2005). However, the applicability of many local scale diversity–invasibility experiments to natural systems has been questioned, because extrinsic factors co-varying with diversity and invasibility in natural systems are typically kept constant in these experiments by design (see review in Fridley et al. 2007). By contrast, in studies where extrinsic factors are allowed to co-vary with diversity, high diversity communities tend to be more heavily invaded, particularly at broader spatial scales (Levine and D'Antonio 1999; Stohlgren et al. 1999; Tilman 2004). Indeed, extrinsic factors, such as resource availability, are thought to explain why the negative relationship between diversity and invasibility, evident primarily in experimental settings, becomes positive in natural communities (Wardle 2001; Hooper et al. 2005; Ortega and Pearson 2005). In short, increases in resource availability can promote both native diversity and invasion (Huston 2004), potentially overriding the buffering effect of diversity on invasion that is evident when resource levels are held constant.

Disturbance is a common force that can increase resource availability, thereby facilitating invasion (Hobbs 1989; Hobbs and Huenneke 1992; Huston 1994; Burke and Grime 1996; Hierro et al. 2006), potentially across diversity levels (Davis et al. 2000; Wardle 2001). A disturbance, such as fire, for example, can remove litter accumulation and allow for increased invader growth (Knapp and Seastedt 1986; Baruch and Bilbao 1999). More efficient resource capture by the invaders over natives (Funk and Vitousek 2007) may also favour invader growth after a disturbance (Huston 2004). Hence, by increasing resource availability, disturbance may shift the diversity–invasibility relationship evident in experimental settings from negative to neutral (Davis et al. 2000; Wardle 2001). That is, disturbance may increase resource availability to a point where, even at high diversity, resources are no longer limiting to invaders, as seen in studies where the influence of resource availability on invasibility swamps diversity-based resistance to invasion (e.g., Davis et al. 2000). Similarly, studies show that diversity confers resilience on communities faced with disturbance (Tilman and Downing 1994; Hector et al. 2010; van Ruijven and Berendse 2010), but it is unclear whether this relationship might hold when communities are also faced with invasion.

While many studies have examined various interactions between diversity, disturbance, and invader success (see review in Hobbs and Huenneke 1992), a key question that has received little attention is whether local-scale diversity continues to impede invader success even after disturbance or, by contrast, whether disturbance creates an invasion "window" (Johnstone 1986) that promotes invader success equally across diversity levels. We are aware of two observational studies addressing this question. One study in a forested system found that canopy disturbance was a more important predictor of invasibility than was diversity (Eschtruth and Battles 2009), but did not examine the interactive effects of diversity, invasion, and disturbance on the native community. Another study in a grassland system found that highly productive areas with high diversity were more heavily invaded after wildfire than were low productivity areas with low diversity (Harrison et al. 2003). However, given that extrinsic factors, such as propagule pressure and resource gradients, were not controlled for in these studies, it is unclear whether diversity drove the observed invasibility patterns. Furthermore, as with the majority of diversity–invasibility studies, these examples examined invader success, yet did not explicitly examine impacts of invaders and disturbance on the native community (Levine et al. 2003).

As it is invader impact which is relevant to natural communities, and not necessarily invader abundance itself (Levine et al. 2003), recent studies have focused on factors that underlie invader impact (Pysek et al. 2012). At a local scale, factors such as diversity of the resident species, invader abundance, or exotic species identity may influence invader impact. We are aware of only three studies that have evaluated the relationship between local-scale diversity and invader impact. These experiments found that invasibility decreased at higher diversities, while invader impact either decreased (Dukes 2002; Maron and Marler 2008a) or increased (Zavaleta and Hulvey 2004) with native diversity. Thus, it remains unclear whether invader

impact scales with invader abundance across diversity levels when extrinsic factors are held constant. The identity of the exotic species may also influence invader impact since exotics differ in their strength of invasion (Ortega and Pearson 2005) and their competitive abilities (Maron and Marler 2008b). Although studies across many types of systems have examined invader impacts at local, community, and ecosystem levels (Pysek et al. 2012), few have examined how factors such as diversity and exotic identity may influence the post-disturbance impact of invaders on native abundance. Understanding these interactions could have important ramifications for how systems are managed, particularly informing the use of disturbances, such as fire, as tools for managing native and exotic abundance (Hobbs and Huenneke 1992).

We experimentally examined the local-scale influence of disturbance on invader abundance and impact across a gradient of native species richness, using previously constructed grassland assemblages. Past work with these assemblages demonstrated that: (1) less diverse assemblages were more invaded, (2) *Centaurea stoebe* (spotted knapweed) was a more potent invader than *Potentilla recta* (sulphur cinquefoil) and *Linaria dalmatica* (Dalmatian toadflax), and (3) invader impact scaled linearly with invader abundance (Maron and Marler 2007, 2008a, b). In the current study, we compared invader and native cover between experimentally disturbed and undisturbed assemblages that represented a range of diversity and exotic identity treatments from the initial study. These analyses allowed us to examine whether invaders or natives were favoured by the disturbance treatment, a combination of drought and fire typically faced by local grasslands. Furthermore, by contrasting native cover in invaded and uninvaded subplots, we assessed the impact of focal exotics on natives across the diversity gradient, in the presence versus absence of experimental disturbance.

## Methods

### Study system

We used experimental plant assemblages, which were originally built in a fallow field at Fort Missoula in 2003, to mimic natural bunchgrass communities, varying in native species richness, in the surrounding Missoula Valley, Montana USA. The native species included three bunchgrasses and thirteen forbs (for species and functional group identity, see Appendix 1 in Electronic Supplemental Material). Native species were chosen to represent a range of flowering times throughout the growing season and various depths of resource uptake. The three exotic species used, *C. stoebe*, *L. dalmatica*, and *P. recta*, are all recognized as noxious weeds in western North America (Rice 2014) and are common in the Missoula Valley. *C. stoebe* (Asteraceae) blooms late season and has a large taproot. *L. dalmatica* (Scrophylariaceae) is a midseason forb with a woody root crown and lateral roots. *P. recta* (Rosaceae) also blooms midseason, but has a single woody crown or a deep taproot.

The results of the first portion of this study, which examined the influence of diversity on invasibility and invader impact, have been published elsewhere (Maron and Marler 2007, 2008a, b). The second portion of the study, described here, examined the influence of disturbance on diversity–invader impact relationships. The disturbance treatment (disturbed by drought/fire, $n = 30$; or not disturbed, $n = 22$) was applied to plots representing a range of native species richness levels (2–10 species at the start of the current study). Subplots within each plot represented each of four previously applied invasion treatments (uninvaded or invaded by *C. stoebe*, *L. dalmatica*, or *P. recta*, respectively). We examined the effects of these three treatments, and their interactions, on native and exotic abundance.

### Experimental design: initial study

In the spring of 2003, experimental plant assemblages ($n = 72$) consisting of $3 \times 3$ m plots were established by transplanting greenhouse-reared native seedlings grown from locally collected seeds. Each plot was divided into four $1.3 \times 1.3$ m subplots separated by 0.4 m buffer strips (Fig. 1), and each subplot was planted with an identical species mix at the same initial density to represent one of 12 diversity treatments (Appendix 1 in Electronic Supplemental Material). Diversity treatments ranged in the number of native species (2–16) and functional groups (1–6), comparable to richness documented in natural grassland communities in the region (Maron and Marler 2008a). That is, each plot had an assigned species richness composed of selected species, and subplots

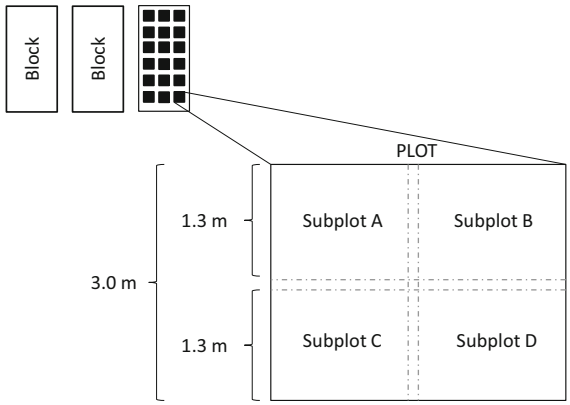


**Fig. 1** Plots were arranged into three blocks. An entire plot, represented by the *black square*, had the same native species richness and composition. Plots were planted with an assigned richness from 2 to 16 native species (Appendix 1 in Electronic Supplemental Material for species list). Plots were divided into four equally sized subplots (*grey dashed lines*), separated by a 40 cm buffer. The invasion treatments, randomly applied to the subplots, included knapweed (*Centaurea stoebe*), toadflax (*Linaria dalmatic*), cinquefoil (*Potentilla recta*) and native (uninvaded). Disturbance (drought/fire or not) was applied at the plot level

therein were weeded several times throughout each growing season to maintain the assigned composition. Buffer strips between subplots were also weeded of all plants. Plots were arranged in three blocks distributed across a fairly homogeneous tilled and fallow field, with plots separated by 3 m within blocks, and blocks separated by 6 m.

After two growing seasons, in the fall of 2004, three invasion treatments were randomly assigned to separate subplots within each plot. Subplots were invaded with either 10.71 g of *C. stoebe* seeds, 0.76 g of *L. dalmatica* seeds, or 0.85 g of *P. recta* seeds, which represented the same number of seeds of each exotic. The fourth subplot in each plot was left uninvaded (hereafter referred to as the native subplot). In September 2005, to ensure propagule pressure was not limiting, subplots were reinvaded with half as many seeds of the same exotic species added in 2004. For each exotic species, total seed weight added across 2004/2005 corresponded to 7500 seeds in each assigned subplot. Subplots were weeded several times per growing season to maintain the assigned exotic and native species composition.

From 2004 to 2007, half of the plots at each level of diversity received a water addition treatment during the growing season as part of previous work. This work showed that there was no significant independent or interacting effect of the water treatment on native biomass, biomass of *L. dalmatica* or *P. recta*, or their impact on natives (Maron and Marler 2008a, b), although watering promoted *C. stoebe* biomass but not its impact (Maron and Marler 2007). In the present study, we assigned former un-watered and watered plots equally between disturbance treatments, but did not include water addition as a factor in our analyses.

## Experimental design: current study

For the current study, which began in 2009, we randomly assigned a subset of 30 plots (stratified by the historic water treatment) across all three blocks to an experimental disturbance treatment and 22 plots across all three blocks to a no-disturbance control. These plots represented a range of the original diversity treatments. Specifically, species richness, as measured in uninvaded subplots in 2009, ranged from 2 to 10 native species and 1 to 5 native functional groups in both disturbed and undisturbed plots. The average $\pm$ SE species richness for uninvaded subplots in 2009 was 5.1 $\pm$ 0.3 species. These 2009 levels of richness are the baseline used for the current study and provide a range of diversity treatments, albeit constrained relative to the original treatments due to species loss.

The disturbance treatment was applied at the plot level in 2009, and consisted of a drought followed by a burn. Drought and fire are disturbances common to grasslands in the intermountain west (Axelrod 1985), and fire typically occurs in conjunction with drought (Westerling et al. 2006) in late summer when lightning strikes ignite dry and senesced vegetation (Old 1969; Kozlowski and Ahlgren 1974). To impose the drought portion of the disturbance treatment, each time it rained during April–June, which spans the wet season in our region, we covered plots with 4.5 $\times$ 4.5 m clear plastic tarps (>80 % light transmittance) that were suspended above plots with bungee cords connected to 1 m tall metal fence posts. Tarps reduced rainfall over the treatment period from an average of 9.1 $\pm$ 0.3 to 2.1 $\pm$ 0.3 cm per plot. Our drought treatment produced an appreciable reduction in rainfall despite the fact that ambient rainfall was below the average historical level of 12.2 cm (based on data for April–June, 1948–2005, obtained from the Western Regional Climate Center: http://www.wrcc.dri.edu/). To impose

the fire portion of the disturbance treatment, in August 2009, we used hand-held drip torches to light one side of the plot and ensured the entire plot burned. The prescribed burn was of low intensity and applied in late-summer, to mimic typical grassland fires in our region (Fischer and Bradley 1987).

### Data collection

We used a 1 $m^2$ quadrat placed at the center of each subplot (uninvaded or invaded by *C. stoebe*, *L. dalmatica*, or *P. recta*) to estimate percent cover for three variables: (a) native grasses, (b) native forbs, and (c) the focal invader. Quadrats were divided into 25 equally sized cells to guide ocular estimation of canopy cover to the nearest percent. We assessed cover during the peak of the growing season in June 2009, which was partway through the drought treatment and prior to the burning. We measured cover of each variable again in June 2011, 2 years after the disturbance, to determine treatment effects. For data analysis, native cover was calculated as the sum of grass and forb cover per subplot in each sampling year.

### Data analysis

We used generalized linear mixed models (SAS version 9.2, GLIMMIX procedure) to examine the response of assemblages to an experimental disturbance (disturbed by drought/fire or not) as a function of native species richness and invasion (uninvaded or invaded by *C. stoebe*, *L. dalmatica*, or *P. recta*) treatments. As explained below, separate models were run for each sampling year representing either pre-disturbance (2009) or post-disturbance conditions (2011). For each sampling year, response variables were either invader cover, as measured for the focal exotic species sown in the subplot, or native cover per subplot. Native species richness, as measured in 2009, prior to the application of the fire treatment, was considered a continuous covariate (range 2–10 species) in these models, and disturbance, invasion, and the interaction of all three treatments were considered fixed factors. Block and plot, nested within block, were considered random factors in all models. Response variables (invader and native cover) were modeled with a beta distribution after applying a standard transformation to account for zeros: $(y \times (n - 1) + 0.5)/n$, where y is cover expressed as a proportion and n is the total sample size (Cribari-Neto and Zeileis 2010). We present least squares means and associated standard errors in the Results to properly account for random factors and the non-normal distribution of cover variables.

To determine if there were any pre-treatment differences between plots assigned to the experimental disturbed versus undisturbed treatments, we first tested response variables measured in 2009 prior to burning. The first of these response variables, invader cover in invaded subplots, did not differ between disturbance treatments ($F_{1,45} = 0.6$, $P = 0.45$), nor were any of the interactions between disturbance and richness or exotic identity significant (for two-way and three-way interactions, $F_{1,45–91} < 0.7$, $P > 0.5$). Similarly, our second response variable, native cover, did not differ between experimental disturbance treatments in 2009 ($F_{1,45} = 0.03$, $P = 0.86$), nor were interactions between disturbance and richness or invasion treatments significant (for two-way and three-way interactions, $F_{1,45–138} < 1.4$, $P > 0.2$).

Given that there were no differences in cover variables by disturbance treatment across richness and invasion treatments in 2009, we conducted our main analyses in the most straightforward manner possible by comparing post-disturbance invader or native cover, as measured in 2011, among the experimental treatments. We conducted three separate analyses that compared: (1) invader cover in invaded subplots among richness, disturbance, and exotic identity treatments (i.e., invaded by *C. stoebe*, *L. dalmatica*, or *P. recta*), (2) native cover in all subplots among richness, disturbance, and invasion treatments, and (3) native cover in uninvaded subplots among richness and disturbance treatments to better elucidate the baseline response of the native community. Initial models included all possible interactions among experimental factors. For analysis of invader cover, we progressively dropped non-significant interactions to obtain the final model. For analyses of native cover, the highest-order interaction was at least marginally significant ($P \leq 0.1$), so we did not drop any interactions.

In order to examine how the impact of focal exotics on native cover varied among species richness and disturbance treatments, we used the full-factor model described above (analysis #2), and isolated particular components of the three-way interaction, as follows: to test for impact of each focal invader as a function of

remaining experimental factors, we contrasted least squares means between invaded and uninvaded subplots for each disturbance treatment, at varying levels of richness. For the latter, we selected three points along the line modeled by the richness covariate, specifically at four, six, and eight native species ("low", "medium", and "high" richness, respectively). These levels represent a range of species richness where 96 % of plots fell, and were selected to illustrate how the response to disturbance and invasion varied over the experimental diversity gradient (i.e., to examine interactions between disturbance, invasion and the richness covariate). Similarly, to examine how native cover in uninvaded subplots responded to disturbance at varying levels of diversity (analysis #3 above), we contrasted disturbed and undisturbed treatments at each of the three levels of native richness. We adjusted our $P$ values for each of these comparisons as follows: $P_{\text{adjusted}} = P \times \text{n}$; where "n" is the number of comparisons.

## Results

### Invader cover

Disturbance elevated invader cover ($P < 0.001$; Table 1a; Fig. 2) from an average of 20 ± SE of 3.8 % cover in undisturbed plots to 39 ± 4.7 % cover in disturbed plots. This positive effect of disturbance on invader cover did not differ across the range of species richness or exotic identity treatments (from the full model: disturbance × richness: $F_{1,69} < 0.1$, $P = 0.96$; disturbance × exotic species: $F_{2,94} = 3.9$, $P = 0.34$; disturbance × richness × exotic species: $F_{2,94} = 1.2$, $P = 0.31$). However, invader cover decreased significantly with native species richness ($P < 0.001$) and also differed among exotic species ($P < 0.001$; Table 1a), with *C. stoebe* the most successful invader, followed by *L. dalmatica* and then *P. recta* (Fig. 2). Furthermore, the focal exotics had different responses to the richness gradient (rich-

**Table 1** Summary statistics from experimental grassland assemblages in Missoula, Montana USA, generated from generalized linear mixed models for three separate response variables: (a) invader cover in invaded subplots, (b) native cover in uninvaded subplots, and (c) native cover in all subplots (invaded and uninvaded)

| | *df* | *F* | *P* |
|---|---|---|---|
| (a) Invader cover (invaded subplots, reduced model) | | | |
| Disturbance | 1, 50 | 17.1 | <0.001 |
| Richness | 1, 58 | 12.4 | <0.001 |
| Exotic identity | 2, 98 | 9.4 | <0.001 |
| Richness × exotic identity | 2, 98 | 3.5 | 0.034 |
| (b) Native cover (uninvaded subplots, full model) | | | |
| Disturbance | 1, 46 | 10.8 | 0.002 |
| Richness | 1, 46 | 12.0 | 0.001 |
| Disturbance × richness | 1, 46 | 8.2 | 0.006 |
| (c) Native cover (all subplots, full model) | | | |
| Disturbance | 1, 44 | 3.9 | 0.056 |
| Richness | 1, 42 | 21.1 | <0.001 |
| Invasion | 2, 138 | 10.8 | <0.001 |
| Disturbance × richness | 1, 41 | 0.8 | 0.36 |
| Disturbance × invasion | 3, 138 | 1.3 | 0.27 |
| Richness × invasion | 3, 138 | 4.9 | 0.003 |
| Disturbance × richness × invasion | 3, 138 | 2.1 | 0.10 |

In all cases, we tested for individual and interacting effects of disturbance (categorical: drought/fire versus control) and native species richness (continuous covariate measured in 2009: range 2–10 species). Additionally, for (a), we considered the effect of exotic identity (*Centaurea stoebe*, *Linaria dalmatica*, or *Potentilla recta*) and for (c), the effect of invasion (uninvaded or invaded by one of the three focal exotics). See text for model details

ness × exotic identity: $P = 0.034$; Table 1a). That is, the negative relationship between invader cover and richness was steepest for *C. stoebe*, followed by *L. dalmatica* and then *P. recta*, and differences in cover among species generally diminished with increasing richness (Fig. 2).

## Native cover

In uninvaded subplots, native cover overall was lower in disturbed than undisturbed plots ($P = 0.002$) and increased with richness ($P = 0.001$; Table 1b; Fig. 3). However, richness buffered native cover against the negative effect of disturbance, as revealed by the significant interaction between disturbance and richness ($P = 0.006$; Table 1b). Specifically, mean native cover was modestly depressed in disturbed relative to undisturbed plots at low richness (contrast: $t_{46} = -3.2$, $P = 0.009$), but not at medium (contrast: $t_{46} = 0.1$, $P > 0.9$) or high richness ($t_{46} = 1.8$, $P > 0.9$).

These overall patterns were similar when we included both invaded and uninvaded subplots in the analysis: native cover was marginally lower in disturbed than undisturbed assemblages ($P = 0.056$), and native cover increased with increasing richness ($P < 0.001$; Table 1c; Fig. 3). However, invasion had strong effects on native cover that interacted with both richness and disturbance. Native cover was lower in subplots invaded by a focal exotic relative to uninvaded subplots overall ($P < 0.001$), but the strength of invader impacts, as measured by the difference in mean native cover between invaded and uninvaded subplots, decreased significantly with richness, signifying a buffering effect of richness against invader impact (richness × invasion: $P = 0.003$; Table 1c; Fig. 3). However, this negative relationship between invader impact and richness was sensitive to disturbance, as suggested by the marginally significant three-way interaction among these factors (richness × invasion × disturbance: $P = 0.10$; Table 1c). Specifically, richness provided a buffer against invader impact in undisturbed but not disturbed plots, as evidenced by comparison of mean native cover between invaded and uninvaded subplots (Fig. 3). That is, in undisturbed assemblages, the invaders *C. stoebe* and *L. dalmatica* significantly depressed native cover at low richness (contrasts: $t_{138} = -5.4$, $P < 0.006$ and $t_{138} = -3.8$, $P = 0.001$, respectively) but not at medium (contrasts: $t_{138} < 2.4$ $P > 0.1$) or high richness (contrasts: $t_{138} < 1.5$, $P > 0.9$), and *P. recta* did not significantly impact native cover at any richness level (contrasts: $t_{138} < 2.0$, $P > 0.3$; Fig. 3a). In contrast, in disturbed assemblages, all three invaders significantly impacted native cover at all levels of richness (contrasts: $t_{138} > 4.3$, $P < 0.001$; Fig. 3b). Invader impacts, when significant, were substantial for all focal exotics, achieving reductions

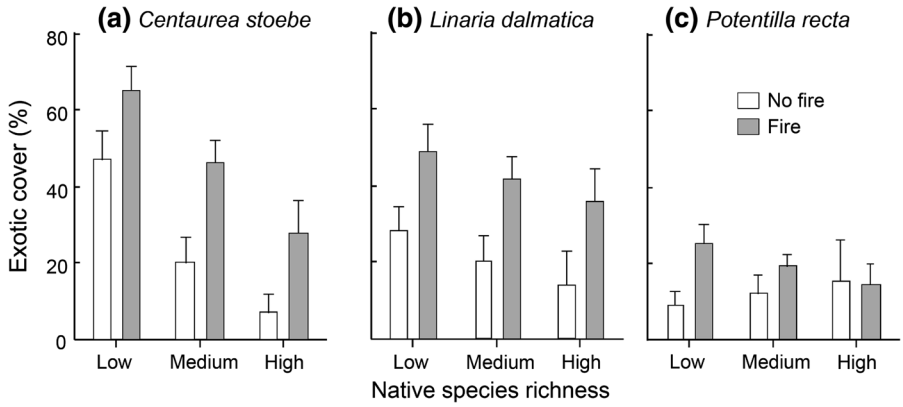


**Fig. 2** Effect of native species richness and an experimental disturbance (applied in 2009) on the percent cover of three exotic species (least squares means + SE from full model), measured in 2011 in experimental assemblages in Missoula, Montana USA. Native richness in 2009 was a continuous covariate in the generalized linear mixed model; to examine the effects of disturbance and exotic identity across this covariate (i.e., interactions between disturbance, exotic identity, and richness), we output least squares means at three levels of richness: low (four species), medium (six species), and high (eight species). These levels were selected for illustrative purposes to represent the range of species richness where 96 % of plots fell

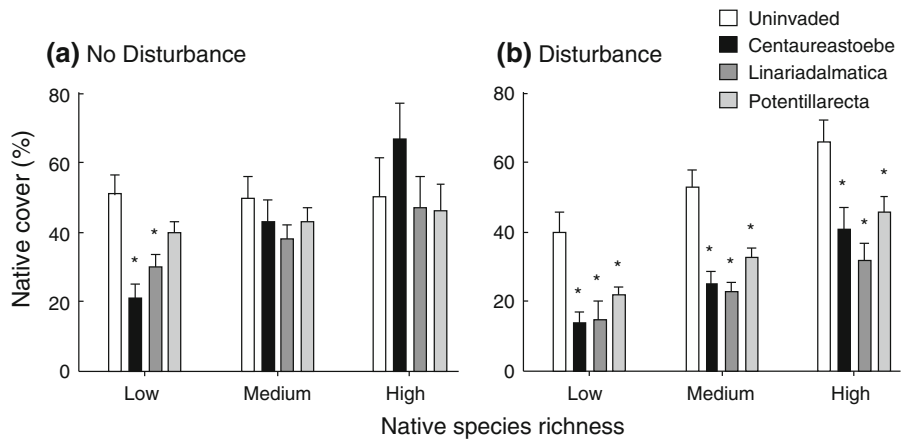


**Fig. 3** Effect of native species richness, invasion, and experimental disturbance on the percent cover of native species (least squares means + SE) in experimental grassland assemblages in Missoula, Montana USA. Invader impact and its interaction with richness and disturbance were assessed by comparing the least squares means for native cover between invaded and uninvaded subplots in differing richness and fire treatments. Native richness in 2009 was a continuous covariate in the generalized linear mixed model. To examine variation in invader impacts across this covariate in both disturbed and undisturbed plots (i.e., interactions between invasion, disturbance, and richness), we conducted contrasts at three levels of richness: low (four species), medium (six species), and high (eight species). These levels were selected for illustrative purposes to represent the range of species richness where 96 % of plots fell. *Asterisks* above invasion treatments indicate significant invader impacts on native cover ($P < 0.05$)

in absolute native cover of 18–34 % across richness and disturbance treatments.

## Discussion

Although theory and empirical work indicate that diversity mediates changes in plant communities spurred by either invasion (e.g., Tilman 1997; Dukes 2002) or disturbance (Tilman and Downing 1994; Hector et al. 2010) in isolation, it is unclear whether diversity remains important in communities faced with both invasion and disturbance. We found that native species richness provided a buffer to community change in three ways: (1) native cover in uninvaded assemblages was depressed by experimental disturbance at low richness, but not higher richness levels; (2) invader cover declined with increasing richness regardless of disturbance, although the strength of the relationship varied with exotic identity; and (3) in the absence of experimental disturbance, invader impacts on native cover diminished at higher richness levels. However, this diversity-based resistance to invader impacts was lost in disturbed assemblages, where invaders depressed native cover at all levels of richness. Hence, species richness helped native assemblages to resist disturbance or invader impact when these forces were faced in isolation, but the combination of disturbance and invasion acted together to overcome this resistance and strongly reduce native cover even at high richness levels.

Native richness provided a buffer to disturbance in uninvaded assemblages, likely by ensuring the presence of species resistant to the drought/fire treatment we imposed. Our low richness assemblages contained only native bunchgrasses (*Festuca idahoensis* and *Koelaria macrantha*), while higher richness assemblages included increasing numbers of forb species, mimicking the fact that these bunchgrasses are dominant species in native grasslands of our region, while diversity in these grasslands is driven by forbs (Lackschewitz 1991). Accordingly, further examination of our data shows that, native grass cover did not vary across the experimental richness gradient ($F_{1,41} = 0.4$, $P = 0.53$), while native forb cover increased with richness ($F_{1,42} = 15.7$, $P < 0.001$). Moreover, native grass cover was suppressed by our disturbance treatment ($F_{1,39} = 38.8$, $P < 0.001$), but native forb cover was not ($F_{1,45} = 0.6$, $P = 0.45$). The differential response of grasses and forbs to our experimental disturbance parallels the response of these taxa to wildfire in our region (Antos et al. 1983).

Furthermore, the drought portion of the disturbance treatment may have compounded the effects of the fire by hastening the senescence of grasses that, unlike native forbs, maintain significant above ground biomass year-round. Thus, in our study, the native response to disturbance at low richness levels appeared to have been driven by bunchgrasses, whereas higher richness assemblages contained forbs that were less susceptible to disturbance. These native forbs thereby conferred diversity-based resistance to disturbance in the absence of invasion. In our system, maintenance and restoration of forb diversity may become an increasingly important management goal as climate change increases fire probabilities at mid- to high-latitudes (Moritz et al. 2012).

Diversity also buffered against invader impact in the absence of disturbance. Specifically, we found that in undisturbed plots, only low diversity assemblages sown with the exotic forbs *C. stoebe* or *L. dalmatica* (but not *P. recta*) experienced significant decreases in native cover relative to uninvaded subplots seven years after invasion, while higher diversity assemblages resisted impact by all three focal invaders (Fig. 3a). Previous work in our experimental system conducted 3 years after invasion and prior to the disturbance treatment also found greater invader impact in low diversity assemblages (Maron and Marler 2008a). Similar patterns were recorded by Dukes in grassland assemblages in California, USA, one year after invasion by the exotic forb *Centaurea solstitialis* (2002; but see Zavaleta and Hulvey 2004). We note that few studies have looked beyond the diversity–invasibility relationship to consider variation in invader impacts as a function of diversity, or considered long-term invader impacts (i.e., more than 3 years) and the persistence of diversity's buffering effect. Other studies have examined the impacts of invaders on native diversity (e.g., Hulme and Bremner 2005; Hejda et al. 2009), but few considered whether invader impact varies with community diversity (see review in Pysek et al. 2012). Our results indicate that when background factors are held constant, local scale diversity can serve to resist invader abundance and impact seven years after invasion, potentially by limiting resources available to invaders (e.g., Tilman 2004; Naeem et al. 2000).

However, native communities frequently face both invasion and disturbance (e.g., Hierro et al. 2006). We found that disturbance exacerbated invader impacts on native cover and overrode the buffering effects of diversity to depress native cover even in high richness assemblages. Hence, disturbed assemblages at all diversity levels experienced impacts by all three exotic species. These results suggest that support the "driver" model of invasion (MacDougall and Turkington 2005) at low diversities, where the native community experienced invader impact regardless of the disturbance. The "passenger" model suggests that external forces, like disturbance, cause both invader success and native decline (MacDougall and Turkington 2005). Here, we found that disturbance alone did not cause native decline at high diversities, although disturbance did increase invader success and impact. Thus, it was the interactive effect of invasion and disturbance that caused native decline. In an observational study, Harrison et al. (2003) found a negative diversity–invasibility relationship after a wildfire, however, neither the diversity gradient nor propagule pressure were manipulated in this study. We know of no previous study examining relationships among resident community diversity, invader impact, and disturbance within an experimental setting (i.e., where these factors were manipulated and extrinsic factors held constant). Our results emphasise the need for land managers to consider the interactive effects of the multiple pressures faced by plant communities.

Like many studies examining these factors in isolation at local scales, we found that invader success (Naeem 2002; Hooper et al. 2005), as well as invader impact (Dukes 2002; Maron and Marler 2008a), were suppressed by diversity and that invaders were facilitated by disturbance (Burke and Grime 1996; Harrison et al. 2003; Hierro et al. 2006). In the absence of disturbance, high diversity communities may resist invasion and associated invader impacts due to a more complete use of resources than achieved at low diversity (Lavorel 1999; Fargione et al. 2003; Tilman 2004). This diversity based resistance to invasion appeared to falter under disturbed conditions, particularly as measured by impacts on native cover. This suggests that the invaders may have pre-emptively taken advantage of resources released by the disturbance (Davis et al. 2000), spurred by the superior ability of exotics to take advantage of these conditions (Funk and Vitousek 2007; Maron et al. 2012).

The invaders in our study may have differentially benefited from a late-summer fire because of their rapid growth and phenologies that extend later in the

year relative to native species' (Wolkovich and Cleland 2011; Pearson et al. 2012). These factors may allow exotics to more readily capture resources made available by disturbance (Sheley et al. 1998). Several observational and experimental studies of exotics from the same genera examined in our study showed an increase in abundance of these taxa after fire (Jacobs and Sheley 2003; Lesica and Martin 2003; Pearson et al. 2012; but see Emery and Gross 2005; Besaw et al. 2011), with unknown effects on invader impacts. In contrast to the exotics most natives in our system senesce by late summer and hence tended to burn more easily, as evidenced by the negative effect of our disturbance treatment on native cover (driven by bunchgrasses). Experimental drought imposed prior to burning may have hastened this effect for natives, whereas the focal exotics tend to remain green and flower late into the summer even when faced with drought (Ortega et al. 2012; Pearson et al. 2012) and may sometimes benefit directly from drought (Coupland et al. 1963; Berube and Myers 1982). Hence, disturbance differentially benefitted the invaders over natives in our study and allowed for increased impact of invaders on natives, potentially because invaders were more efficient at using resources made available by the disturbance. This exacerbation of invader impact was particularly relevant at higher levels of richness where impact was not evident in the absence of disturbance. Our results suggest that before the application of landscape management tools (e.g., controlled burning) decision makers need to consider not just native ecosystem response, but also potential undesirable effects disturbance on existing communities, including exacerbation of invader impacts.

Despite the fact that both invader cover and impact were generally greater in disturbed than undisturbed plots, our results demonstrate that invader impact does not necessarily scale directly with invader cover after disturbance. Although there were substantial differences in cover among the three exotics and across the richness gradient, their impacts on natives were nevertheless comparable across these conditions in disturbed plots (Fig. 3b). For example, *P. recta* had the lowest cover of the three exotics, yet had strong impacts on natives in disturbed plots. Similarly, *C. stoebe*, the most abundant invader, dropped in cover by about 60 % in low relative to high richness assemblages but caused a comparable reduction in native cover across the richness gradient. These patterns suggest that disturbance allowed the invaders to cross a threshold in cover, beyond which impact on native cover was constant. In contrast, previous studies in undisturbed assemblages found that invader impact, measured as the proportional difference in native biomass between invaded and uninvaded assemblages, scaled linearly with exotic biomass (Maron and Marler 2008a). Differences in impact among invaders across a richness gradient were attributed to differences in invasibility rather than change in per capita impacts (Maron and Marler 2008a). In the current study, resource pre-emption by the invaders under disturbed conditions (Davis et al. 2000; Funk and Vitousek 2007) may have allowed invader cover to cross a threshold after which native richness or exotic identity no longer influenced the degree of impact on native cover.

Our study supports the finding that some invasives thrive after disturbance (e.g. Hobbs and Huenneke 1992; Hierro et al. 2006). We showed that experimental disturbance mimicking a natural drought/fire event did not fundamentally alter the negative relationship between local native diversity and invader cover documented in numerous studies. Rather, disturbance elevated cover of exotic perennial forbs to a similar degree across a gradient of species richness levels. However, we found that disturbance increased the impact of these invaders on native cover, particularly at higher levels of species richness, such that diversity no longer buffered communities against invader impact. Hence, although diversity suppressed invader abundance, even high diversity communities were vulnerable to invader impacts after a disturbance. The compound effect of invasion and fire on natives could thus potentially create an alternative stable state where communities are dominated by exotic species (Scheffer and Carpenter 2003).

As invaders can benefit from natural disturbances, such as a fire, and disturbance regimes may be altered by climate change, it will become increasingly important for land managers to consider the complexities of interacting anthropogenic pressures (Huston 2004). Our results suggest that although diversity can provide a buffer against invasion and disturbance when faced in isolation, local diversity is not enough to buffer against these combined pressures. Thus using controlled burning to promote maintenance and restoration of native landscapes must be carefully considered in light of potential negative impacts of

invaders on native communities. Future studies should examine whether these patterns are consistent in other systems or with different disturbances.

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## References

Antos JA, McCune B, Bara C (1983) The effect of fire on an ungrazed Western Montana grassland. Am Midland Nat 110:354–364

Axelrod DI (1985) Rise of the grassland biome, Central North-America. Bot Rev 51:163–201

Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C4 grasses in a Neotropical savanna. Oecologia 119:510–520

Berube DE, Myers JH (1982) Suppresion of knapweed invasion by crested wheatgrass in the dry interior of British Columbia. J Range Manag 35:459–461

Besaw LM, Thelen GC, Sutherland S, Metlen K, Callaway RM (2011) Disturbance, resource pulses and invasion: short-term shifts in competitive effects, not growth responses, favour exotic annuals. J Appl Ecol 48:998–1006

Burke MJ, Grime JP (1996) An experimental study of plant community invasibility. Ecology 77:776–790

Coupland RT, Zilke S, Sellec GW (1963) Spread of toadflax in Saskatchewan. Can J Plant Sci 43:214–221

Cribari-Neto F, Zeileis A (2010) Beta regression in R. J Stat Softw 34:1–24

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dukes JS (2002) Species composition and diversity affect grassland susceptibility and response to invasion. Ecol Appl 12:602–617

Emery SM, Gross KL (2005) Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. J Appl Ecol 42:60–69

Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol Mono 79:265–280

Fargione JE, Tilman D (2005) Diversity decreases invasion via both sampling and complementarity effects. Ecol Lett 8:604–611

Fargione JE, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Natl Acad Sci 100:8916–8920

Fischer WC, Bradley AF (1987) Fire ecology of western Montana forest habitat types. General technical report INT-223, Forest Service, US Dept of Ag., Ogden, USA

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resoure systems. Nature 446:1079–1081

Harrison S, Inouye BD, Safford HD (2003) Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conserv Biol 17:837–845

Hector A, Hautier Y, Saner P, Wacker L, Bagchi R, Joshi J, Scherer-Lorenzen M, Spehn EM, Bazeley-White E, Weilenmann M, Caldeira MC, Dimitrakopoulos PG, Finn JA, Huss-Danell K, Jumpponen A, Mulder CPH, Palmborg C, Pereira JS, Siamantziouras ASD, Terry AC, Troumbis AY, Schmid B, Loreau M (2010) General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. Ecology 91:2213–2220

Hejda M, Pysek P, Jarosik V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97:393–403

Hierro JL, Villarreal D, Eren O, Graham JM, Callaway RM (2006) Disturbance facilitates invasion: the effects are stronger abroad than at home. Am Nat 168:144–156

Hobbs RJ (1989) The nature and effects of disturbance relative to invasions. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger M, Rejmanek M, Williamson M (eds) Biological Invasions: a global perspective. Wiley, Chichester, pp 389–405

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conserv Biol 6:324–337

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hulme PE, Bremner ET (2005) Assessing the immpact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J Appl Ecol 43:43–50

Huston MA (1994) Biodiversity. Cambridge University Press, Cambridge

Huston MA (2004) Management strategies for plant inasions: manipulating productivity, disturbance, and competition. Divers Distrib 10:167–178

Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. Science 317:58–62

Jacobs JS, Sheley RL (2003) Prescribed fire effects on dalmation toadflax. J Range Manag 56:193–197

Johnstone IM (1986) Plant invasion windows: a time based classification of invasion potential. Biol Rev 61:369–394

Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. Biosci 36:662–668

Kozlowski TT, Ahlgren CE (1974) Fire and ecosystems. Academic Press, New York

Lackschewitz K (1991) Vascular plants of west-central Montana: identification guidebook. US Dept of Ag Forest Service, Intermountain Research Station, Ogden

Lavorel S (1999) Ecological diversity and resilience of Mediterranean vegetation to disturbance. Divers Distrib 5:3–13

Lesica P, Martin B (2003) Effects of prescribed fire and season of burn on recruitment of the invasive exotic plant, *Potentilla recta*, in a semiarid grassland. Restoration Ecol 11:516–523

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond Ser B Biol Sci 270:775–781

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Maron J, Marler M (2007) Native plant diversity resists invasion at both low and high resource levels. Ecology 88:2651–2661

Maron J, Marler M (2008a) Effects of native species diversity and resource additions on invader impact. Am Nat 72:S18–S33

Maron J, Marler M (2008b) Field-based competitive impacts between invaders and natives at varying resource supply. J Ecol 96:1187–1197

Maron JL, Pearson DE, Potter T, Ortega YK (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. J Ecol 100:1492–1500

Moritz MA, Parisen M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K (2012) Climate change and disruptions to global fire activity. Ecosphere 6:1–22

Naeem S (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. Ecology 83:1537–1552

Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108

Old SM (1969) Microclimate, fire, and plant production in an Illinois prairie. Ecol Monogr 39:355–384

Ortega YK, Pearson DE (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. Ecol Appl 15:651–661

Ortega YK, Pearson DE, Waller LP, Surdevant NJ, Maron JL (2012) Population-level compensation impedes biological control of an invasive forb and indirect release of a native grass. Ecology 93:783–792

Pearson DE, Ortega YK, Sears SJ (2012) Darwin's naturalization hypothesis up-close: intermountain grassland invaders differ morphologically and phenologically from native community dominants. Biol Invasions 14:901–913

Pysek P, Jarosik V, Hulme P, Pergl J, Hejda M, Schaffner U, Vila M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Chang Biol 18:1725–1737

Rice, P (2014) Invaders Database System. Divison of Biological Sciences, University of Montana, USA. http://invader.dbs.umt.edu/

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Ev 18:648–656

Sheley RL, Jacobs JS, Carpinelli MF (1998) Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technol 12:353–362

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46

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

Tilman D (2004) Niche tradeoffs, neutraility, and communiy structure: a stochastic theory of resource competition, invasion, and communnity assembly. Proc Natl Acad Sci 101:10854–10861

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. Nature 367:363–365

van Ruijven J, Berendse F (2010) Diversity enhances community recovery, but not resistance, after drought. J Ecol 98:81–86

Wardle DA (2001) Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? Oikos 95:161–170

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943

Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. Front Ecol Environ 9:287–294

Zavaleta ES, Hulvey KB (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. Science 306:1175–1177